

Comparative Review of the Human Bony Labyrinth

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KEY WORDS primates; hominoids; inner ear; semicircular canals; cochlea; locomotion; basicranium

ABSTRACT The bony labyrinth inside the petrous part of the temporal bone houses the organs of hearing and balance. Being functionally linked with sensory control of body movements and located in a part of the basicranium that is closely associated with the brain, this structure is of great interest in the study of human evolutionary history. However, few aspects of its morphology have been studied in nonhuman primates. This review compares the bony labyrinth of humans with that of the great apes and 37 other primate species based on data newly acquired with computed tomography combined with previous descriptions. With body mass taken into account, consistent differences are found between the size of the semicircular canals in humans, the great apes, and other primates. In particular, the arcs of the anterior and posterior canals are larger in humans than in the African apes. The functional implications of semicircular canal dimensions for registering angular head motion are evaluated in relation to locomotor behavior. Biophysical models, comparative studies, and some neurophysiological experiments all support a link between semicircular canal size and agility, or more specifically the frequency contents of natural head movements, but the evidence on the exact nature of this link is ambiguous. It is concluded that any link between the characteristic dimensions of the human canals and locomotion will be more complex than a simple association with the broad categories of quadrupedal vs. bipedal behavior. The functionally important planar orientations of the semicircular canals are similar in humans and the African apes as well as in many other species. In contrast, other aspects of the human labyrinth differ markedly in shape, following a pattern that seems to reflect the characteristic architecture of the human basicranium. Indeed, it is found that labyrinthine and basicranial shape are interspecifically correlated in the sample, and in most respects the human morphology is consistent with the general trend among primate species. Differences in brain growth and development are proposed as the predominant factor underlying both the unique shape of the human labyrinth as well as the interspecific labyrintho-basicranial correlations. *Yrbk Phys Anthropol* 41:211-251, 1998. © 1998 Wiley-Liss, Inc.

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Recent analyses of hominid fossils have demonstrated the great potential of the bony labyrinth to provide evidence on phylogenetic relationships between taxa as well as on aspects of locomotor behavior and basicranial development (Spoor and Zonneveld, 1994a; Spoor et al., 1994; Hublin et al., 1996). Located inside the petrous part of the temporal bone, this relatively unknown structure houses the sense organs for the perception of sound in the cochlea and for registering head movements and orientation in the vestibule and the semicircular canals. Building upon the brief comparisons made in previous studies, this paper presents a more comprehensive analysis of differences between the labyrinths of humans and other extant primates. Its wider aims are to explore primate labyrinthine diversity in relation to basicranial architecture and semicircular canal function and to provide a framework for the interpretation of the hominid fossil record.

Whereas the human bony labyrinth is well known from a large body of literature, ranging from detailed qualitative descriptions (Anson and Donaldson, 1981) to morphometric analyses of population variation (Muren et al., 1986; Dimopoulos and Muren, 1990), few studies have made comparisons with other primate species. Initial comparative observations are given in Hyrtl (1845), a pioneering work on the mammalian middle and inner ear which was among the first to apply the technique of casting the air-filled spaces of the macerated temporal bone. Sub-

sequent studies discuss the labyrinth of individual species, including the great apes other than *Pan paniscus*, with an emphasis on general description rather than systematic interspecific comparison and analysis (Denker, 1899a,b; Berg, 1903; Gray, 1907; Altmann and Vermes, 1933; Takahashi, 1976).

A second group of morphological studies dealing with the primate bony labyrinth focuses on the morphology that has a direct biophysical relationship with the function of the semicircular canal system (Igarashi, 1967; Igarashi et al., 1981; Blanks et al., 1975, 1985; Ramprashad et al., 1984; Matano et al., 1985, 1986; Reisine et al., 1988). This system records angular head movements and, through the vestibular reflexes, plays an important role in the coordination of eye, head, and body movements. Best known among these is perhaps the vestibulo-ocular reflex, which helps stabilize the eyes while making head movements during locomotion, thus avoiding blurred vision. The aspects of the bony labyrinth that are functionally important in this respect are the arc size and planar orientation of the semicircular canals. The plane of each bony canal closely approximates that of the enclosed membranous duct,¹ and both are indicative of, although not identical to, the physiologi-

¹Following the *Nomina anatomica* (International Anatomical Nomenclature Committee, 1983), the term *semicircular canal* refers to the bony morphology and the term *semicircular duct* to the membranous duct inside the canal. The term *semicircular canal system* covers the entire functional unit including both bony and soft-tissue aspects.

cal plane of optimum perceptive sensitivity (Estes et al., 1975; Blanks et al., 1985; Reisine et al., 1988). The semicircular canals are traditionally described as lying in three orthogonal planes, with those of the vertical (anterior and posterior) canals making an angle of approximately 45° with the sagittal plane (e.g., Anson and Donaldson, 1981; Romer and Parsons, 1977). Thus, each anterior canal and contralateral posterior canal are coplanar, forming a functional unit as a synergistic push-pull pair in which excitation of one canal corresponds with inhibition of the other (Graf, 1988). However, the actual planar orientation of the vertical canals in nonhuman primates has been measured for only a few species frequently used in physiological experiments (Blanks et al., 1985; Reisine et al., 1988). The orientation of the lateral canal in the cranium has been discussed in a large number of studies based on the vestibular orientation method, which uses the plane of the canal as the reference orientation in craniometric analyses (for a review see Fenart and Pellerin, 1988). The underlying hypothesis of this approach is that animals hold their heads in such a position that the lateral canals are horizontal (Perez, 1922; Girard, 1923; Lebedkin, 1924; for a critical review see De Beer, 1947). The two lateral canals form a functional push-pull pair among themselves.

The bony canal also provides an estimate of the arc size of the enclosed duct. Together with other factors, such as the endolymph's viscosity and the duct's lumen size, this arc size influences the mechanical response behavior of the semicircular canal system. Most importantly here, changing the dimensions of the ducts has been proposed as a mechanism for tuning the functional characteristics of the system to the frequency spectrum of head movements typical for the locomotor repertoire of an animal (Wilson and Melvill Jones, 1979). If substantiated, a strong link between locomotor patterns and semicircular canal size in extant species would provide powerful tests of inferred locomotor behavior in related extinct taxa independent of those inferred from their postcranial skeleton. The diversity of locomotor behaviors found in extant primates

makes them an ideal group in which to assess this relationship. Indeed, Matano et al. (1985, 1986) found significant differences between the canal sizes of the vertical clinger and leaper *Tarsius* and the slow quadrupedal climber *Nycticebus*. Moreover, Spoor et al. (1994) identified different canal sizes in modern humans compared with the great apes and suggested a possible relationship with habitual bipedalism. It is worth mentioning that, in contrast to the planar orientation and the arc size, the lumen size of the bony semicircular canal is of little biophysical relevance because it does not reliably reflect the functionally important lumen size of the enclosed duct (e.g., Curthoys et al., 1977b; Ramprasad et al., 1984).

A third category of research has explored primate labyrinthine morphology in relation to phylogenetic changes of the cranium (Werner, 1933; Villemain and Beauvieux, 1934; Saban, 1952; Delattre and Fenart, 1960, 1961, 1962; Fenart and Deblock, 1973). Characters assessed in these studies concern angles between the plane of the lateral semicircular canal and structures such as the oval and round windows, the common crus, and the cochlea. Interspecific differences in these angles are associated with aspects of cranial shape, including the degree of midline basicranial flexion and foramen magnum orientation. Based on broad trends observed among mammalian species, Delattre and Fenart (1960, 1961, 1962) concluded that the human labyrinthine shape should be seen as a product of basicranial remodeling, driven by the transition to an upright posture. However, Werner (1933) associated similar changes of labyrinthine angles, which he observed among species of fish, birds, and primates, with different patterns and degrees of brain development. Based on a preliminary review of primate labyrinths, Spoor and Zonneveld (1994a) found support for human characteristics identified in Delattre and Fenart's studies and also noticed a possible association between the lateral canal shape and the coronally oriented petrous pyramids in humans.

It is the possible links with locomotor behavior, body posture, basicranial remodeling, and brain development that make the comparative analysis of the human bony

labyrinth of particular interest, because all of these aspects play a crucial role in human evolutionary history. In addition, it has been shown that, as a purely practical application, the morphological analysis of the labyrinth can be used to assess the phylogenetic affinities of fossil hominid specimens (Spoor et al., 1994; Hublin et al., 1996). In this respect an improved insight into the labyrinthine diversity among extant hominoids and other primates will greatly help in selecting useful characters.

This review compares the bony labyrinth of modern humans with that of the great apes as well as a range of other primate species. The latter are included to provide a broad overview of primate labyrinthine morphologies rather than to study the individual taxa. The analyses examine aspects of the labyrinth that are related to semicircular canal function, planar stability and arc size of the canals in particular, as well as possible interrelationships between labyrinthine shape and basicranial architecture. Previous comparative studies of the bony labyrinth were made on the basis of casts, serial sections or microdissections, techniques which greatly limit the availability of material because of their destructive nature. In contrast, the new data presented in this study are based on computed tomography (CT), shown to be an accurate, fast, and noninvasive method for visualizing and morphometrically analyzing the labyrinth in both extant and fossil primates (Spoor and Zonneveld, 1995).

MATERIALS AND METHODS

Sample

Comparisons were made between 42 primate species, based on a total of 296 specimens which were either specifically CT-scanned for this purpose or for which semicircular canal dimensions could be taken from the literature (Table 1). The nonhuman sample that was CT-scanned consists of adult dry skulls of wild-caught animals, with the exception of seven captive specimens (three of *Pan troglodytes*, two of *Macaca fascicularis*, one of *Lagothrix lagotheria*, and one of *Saimiri sciureus*). Of the captive specimens, two of *Pan* and one of *Macaca* were embalmed heads rather than

TABLE 1. Sample analyzed in this study, giving the species codes used in the graphs, and the number of specimens¹

Species	Code	CT	Published
<i>Homo sapiens</i>	Hs	53 (26m, 22f, 5?)	49 (c,g)
<i>Pan troglodytes</i>	Pt	7 (3m, 3f, 1?)	1 (a)
<i>Pan paniscus</i>	Pp	6 (3m, 3f)	—
<i>Gorilla gorilla</i>	Gg	6 (3m, 3f)	1 (a)
<i>Pongo pygmaeus</i>	Po	7 (3m, 4f)	1 (a)
<i>Hylobates syndactylus</i>	Hy	2 (1m, 1f)	—
<i>Hylobates lar</i>	Hi	—	2 (g)
<i>Hylobates moloch</i>	Hm	1 (f)	—
<i>Hylobates pileatus</i>	Hp	1 (m)	—
<i>Macaca fascicularis</i>	Mf	3 (2m, 1f)	27 (f)
<i>Macaca mulatta</i>	Mm	—	15 (b)
<i>Macaca nemestrina</i>	Mn	—	1 (a)
<i>Macaca nigra</i>	Mi	—	1 (d)
<i>Macaca tonkeana</i>	Mt	—	2 (g)
<i>Macaca cyclopis</i>	Mc	—	25 (g)
<i>Macaca fuscata</i>	Mu	—	22 (g)
<i>Papio cynocephalus</i>	Pc	—	1 (d)
<i>Papio hamadryas</i>	Ph	—	1 (a)
<i>Papio ursinus</i>	Pu	1 (f)	—
<i>Theropithecus gelada</i>	Tg	1 (m)	—
<i>Mandrillus sphinx</i>	Ms	1 (m)	—
<i>Cercopithecus aethiops</i>	Ce	—	1 (d)
<i>Cercopithecus nictitans</i>	Cn	—	1 (d)
<i>Cercopithecus mona</i>	Cm	—	1 (a)
<i>Colobus guereza</i>	Cg	1 (m)	—
<i>Presbytis entellus</i>	Pe	1 (f)	—
<i>Nasalis larvatus</i>	Nl	1 (m)	—
<i>Callithrix jacchus</i>	Cj	—	3 (d,g)
<i>Cebus apella</i>	Ca	1 (m)	—
<i>Saimiri sciureus</i>	Ss	1 (?)	25 (b,f,g)
<i>Aotus trivirgatus</i>	At	—	1 (f)
<i>Lagothrix lagotheria</i>	Ll	1 (?)	—
<i>Alouatta seniculus</i>	As	1 (m)	1 (a)
<i>Ateles geoffroyi</i>	Ag	—	2 (g)
<i>Tarsius bancanus</i>	Tb	—	1 (e)
<i>Propithecus diadema</i>	Pd	1 (m)	—
<i>Indri indri</i>	Ii	1 (m)	—
<i>Lemur catta</i>	Lc	—	2 (g)
<i>Eulemur macaco</i>	Ea	—	1 (a)
<i>Eulemur mongoz</i>	Eo	—	1 (d)
<i>Microcebus rufus</i>	Mr	1 (m)	—
<i>Nycticebus coucang</i>	Nc	—	8 (d,e,g)

¹ For the species studied using CT scans (CT), the sex is indicated in parentheses (m, male; f, female; ?, unknown). For the species of which canal dimensions were obtained from the literature (Published), the source is indicated in parentheses, a, Berg, 1903; b, Blanks et al., 1985; c, Curthoys et al., 1977a, b; d, Gray, 1907; e, Matano et al., 1985; f, Ramprasad et al., 1984; g, Takahashi, 1976.

dry skulls. The specimens are from the Rijksmuseum van Natuurlijke Historie (Leiden), the Utrecht University Museum, the Museum voor Midden Afrika (Tervuren), the anatomy departments of the Universities of Amsterdam, Groningen, and The Witwatersrand (Johannesburg), The Royal College of Surgeons (London), and the research collections of the first author and H. Kemperman (Utrecht). The collection numbers are given in Appendix 6.1 of Spoor (1993). The

human sample consists of adult dry skulls from the collections of the anatomy departments of the Universities of Groningen and Leiden, Philips Medical Systems (Best), and the first author. They were selected to obtain maximum geographical diversity, and their region of origin and collection numbers are listed in Appendix 5.1 of Spor (1993).

In a preliminary analysis, the semicircular canals of primates were compared with those of other mammals (45 species representing 15 orders) using measurements listed in Gray (1907, 1908) and taken from a Plexiglas cast of an *Elephas maximus* labyrinth (collection O. Gray, currently in the care of the first author).

Imaging the labyrinth

The method of visualizing the primate labyrinth by CT follows the procedures described in Spor and Zonneveld (1995). All scans except those of *Microcebus* were made with medical high-resolution CT scanners. *Colobus*, *Presbytes*, and *Cebus* were scanned with a Siemens Somatom 4+ (Middlesex Hospital, London), using an exposure of 83 mAs at 130 kVp tube voltage, a 1 mm slice thickness, and a field of view of the images of between 90 and 115 mm (512×512 matrix). All other specimens were scanned with a Philips Tomoscan 350 (Utrecht University Hospital; Rosebank Clinic, Johannesburg), using an exposure of 480 mAs at 120 kVp tube voltage, a slice thickness of 1.5 mm, and a field of view of 240 mm or 80 mm (256×256 matrix) for overview images of the entire cranium and zoom reconstructions of the temporal bone area, respectively.

One labyrinth of each specimen was investigated. Scans were made in the transverse and sagittal planes covering the area of the petrous pyramid, and the sagittal series also includes a midsagittal scan. The transverse plane aims to visualize the full extent of the lateral semicircular canal in a single scan. This could be achieved by scanning in the nasion-biporionic plane, with the exception of the *Indri* specimen, which had to be scanned in a more inclined plane. The scans of the hominoid specimens, *Papio*, *Mandrillus*, and *Nasalis*, were made contiguously, with additional overlapping scans (slice increment 0.75 mm) at the level of the lateral

semicircular canal in the transverse series and at the level of the common crus in the sagittal series. The other specimens were completely scanned with overlapping slices. A slice increment of 0.4 mm was used for *Saimiri*.

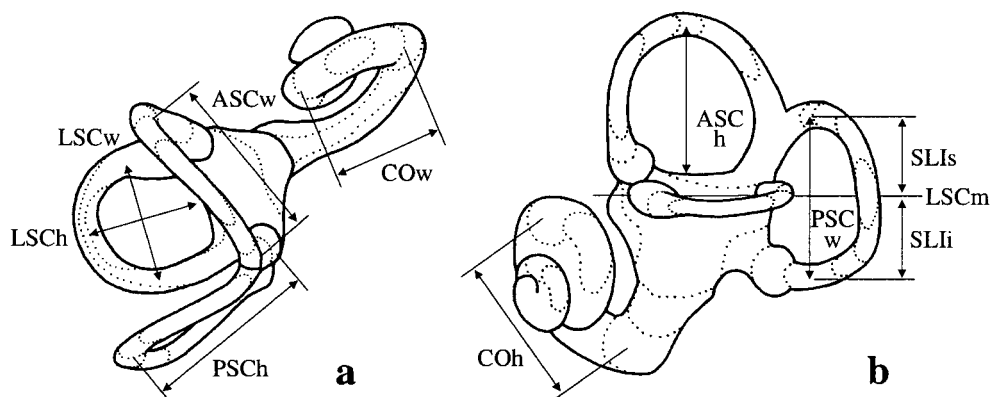
The *Microcebus* cranium was scanned using an experimental micro-CT scanner of the Microfocal X-ray Unit of UMDS Guy's Hospital, London. The scans that were reconstructed in the sagittal and transverse planes have a slice thickness and pixel size of 0.060 mm (J. Lynch and P. Liepins, personal communication).

For an initial quantitative assessment, superior and lateral views of each labyrinth were reconstructed from the transverse and sagittal series of scans, respectively. The appropriate contours that appear in each scan were drawn on the monitor screen, and the combined image was copied onto translucent paper (contours of individual slices are shown in the diagrams of Fig. 1).

Quantitative analysis

Interspecific morphological differences of the bony labyrinth and the cranial base were quantitatively analyzed by taking linear measurements and angles from the CT scans. The labyrinthine measurements, defined in detail in Spor and Zonneveld (1995), are shown in Figure 1 and listed in Table 2 with a brief description and the abbreviations used in the tables and figures. The landmarks of the measurements are located either in the center of the lumen of the semicircular canals and the cochlea or on the wall of the vestibule. The exact position of the landmarks is identified on the basis of the local CT (Hounsfield) values in the scans, a technique described in Spor and Zonneveld (1995) and Spor et al. (1993). The linear measurements were taken to the nearest tenth of a millimeter and the angles to the nearest degree. For the scans used in this study, the accuracy and precision corresponds to a maximum error of these measurements of ± 0.1 mm and $\pm 4^\circ$, respectively (Spor and Zonneveld, 1995). For the micro-CT images, the accuracy is doubtless better, but this has not been tested specifically.

linear dimensions



orientations

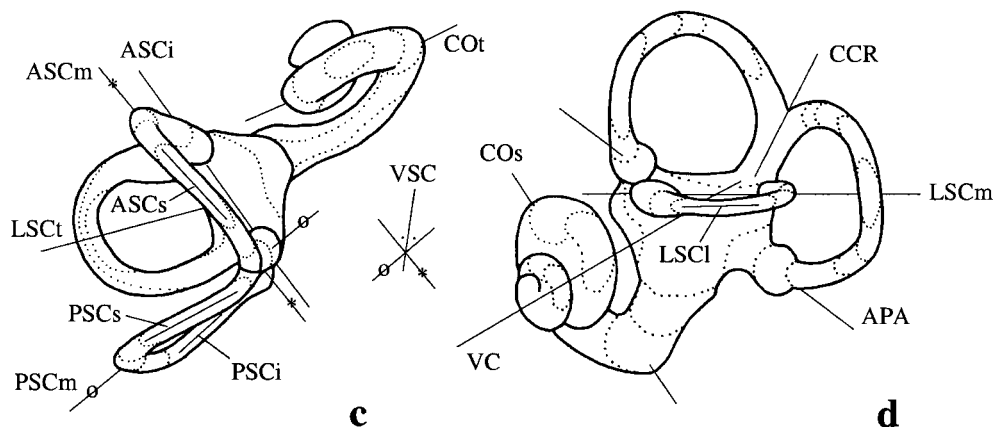


Fig. 1. Superior (a,c) and lateral (b,d) aspects of a left human labyrinth as reconstructed from transverse and sagittal CT scans, respectively, showing the measurements used in this study. Measurement abbreviations are listed in Table 2. The dotted lines represent the outlines of the labyrinth that appear in individual scans.

The linear measurements of the labyrinth include the height and width of the arc of each semicircular canal and of the basal turn of the cochlea (Fig. 1a,b). The height of a semicircular canal is always defined as the largest distance of the arc from the vestibule and its width perpendicular to the height, irrespective of the orientation of the canal in the cranium. No measurements were taken of the lumen size of the canals or the cochlea. Owing to the limitations of the spatial resolution, such dimensions are too small to be

taken from the CT scans with sufficient accuracy (Spoor and Zonneveld, 1995). This restriction is not critical because the lumen size of the cochlea and particularly the bony canals has little functional relevance.

The radius of curvature (R) of each canal arc and of the cochlear basal turn was calculated by taking half the average of the height and width measurements ($0.5[h + w]/2$). Apart from its functional importance in biophysical models of the semicircular canal system, the radius conveniently ex-

TABLE 2. Abbreviations of the linear dimensions and orientations of the labyrinth (Fig. 1) and the petrous pyramid and the midsagittal landmarks of the cranium

Linear dimensions	
ASCh	Height of the anterior semicircular canal (Fig. 1b)
ASCw	Width of the anterior semicircular canal (Fig. 1a)
COh	Height of the basal turn of the cochlea (Fig. 1b)
COW	Width of the basal turn of the cochlea (Fig. 1a)
LSCCh	Height of the lateral semicircular canal (Fig. 1a)
LSCw	Width of the lateral semicircular canal (Fig. 1a)
PSCCh	Height of the posterior semicircular canal (Fig. 1a)
PSCw	Width of the posterior semicircular canal (Fig. 1b)
SLI	The sagittal labyrinthine index, calculated from the dimensions SLIs and SLIi as $SLIi / (SLIs + SLIi) \times 100$ (Fig. 1b)
R	Radius of curvature of a semicircular canal or the cochlear basal turn measured to the center of the lumen ($R = 0.5 \times [\text{height} + \text{width}] / 2$)
R'	Radius of curvature of a semicircular canal measured to outer most wall
Orientations	
APA	The ampullar line connecting the centers of the anterior and posterior ampullae and projected onto the sagittal plane (Fig. 1d)
ASCI	The inferiormost part of the anterior semicircular canal, defined by the line in the transverse plane connecting the apertures of the anterior ampulla and the common crus into the vestibule (Fig. 1c); labelled as "V" in Spor and Zonneveld (1995)
ASCm	The arc of the anterior semicircular canal at its greatest width in the transverse plane (Fig. 1c)
ASCs	The superiormost part of the anterior semicircular canal in the transverse plane (Fig. 1c)
CCR	The common crus in the sagittal plane (Fig. 1d)
COs	The basal turn of the cochlea in the sagittal plane (Fig. 1d)
COT	The basal turn of the cochlea in the transverse plane (Fig. 1c)
LSCI	The lateralmost part of the lateral semicircular canal in the sagittal plane (Fig. 1d)
LSCm	The arc of the lateral semicircular canal at its greatest width in the sagittal plane (Fig. 1d)
LSCt	The axis of symmetry of the lateral semicircular canal in transverse plane (Fig. 1c)
PPp	The posterior petrosal surface in the sagittal plane at the level of the common crus (Fig. 2b)
PPip	The posterior petrosal surface in the transverse plane at the level of the lateral semicircular canal (Fig. 2a)
PSCI	The inferior limb of the posterior semicircular canal in the transverse plane (Fig. 1c)
PSCm	The arc of the posterior semicircular canal at its greatest width in the transverse plane (Fig. 1c)
PSCs	The superior limb of the posterior semicircular canal in the transverse plane (Fig. 1c)
SG	Intersection of the (mid)sagittal plane of the cranium in the transverse plane
VC	The vestibulocochlear line connecting the center of the arc of the lateral semicircular canal and the lateralmost point of the second cochlear turn projected onto the sagittal plane (Fig. 1d).
VSC	Reference line in the transverse plane bisecting the anteroposteriorly opening angle between the arc orientations of the two vertical semicircular canals (ASCm and PSCm; Fig. 1c).
Midsagittal landmarks	
ba	basion
fc	foramen caecum
na	nasion
o	opisthion
s	sella

presses the overall size of each structure. Moreover, additional semicircular canal radii could be obtained from previous studies (Table 1), which makes a wider comparison possible than on the basis of the CT sample alone. These studies either give the radii (Blanks et al., 1985; Matano et al., 1985) or list the dimensions of the canals from which the radii could be calculated (Berg, 1903; Gray, 1907, 1908; Takahashi, 1976; Curthoys et al., 1977a; Ramprashad et al., 1984).

In functional interpretations of semicircular canal size, the measurements of the bony labyrinth aim to provide estimates of the arc size of the enclosed membranous ducts. Given that the duct is located along the

outermost wall of the bony canal rather than in its center (Gray, 1907; Curthoys et al., 1977a; Ramprashad et al., 1984), the accuracy of such estimates is affected by the size relationship between the lumina of the canal and the duct. In primates, this varies from prosimians, with virtually no perilymphatic space surrounding the duct, to humans, in whom the space occupies more than 90% of the canal lumen (Hyrtl, 1845; Gray, 1907; Curthoys et al., 1977b; Ramprashad et al., 1984). Correction factors transforming the radius of curvature of the bony canal into that of the duct can be obtained only for humans and a very few other primates (Curthoys et al., 1977a; Ramprashad

et al., 1984) and are not available for the great apes. With the duct's location in mind, an alternative to taking measurements from the center of the canal could be using landmarks on the outermost wall. However, in CT scans the exact location of the canal wall is difficult to establish, owing to the limitations of the spatial resolution (Spoor and Zonneveld, 1995). Canal radii to the outer wall were therefore examined only for those primate species for which the required measurements, taken from casts and serial sections, could be obtained. Apart from the sources listed in Table 1, canal lumen diameters listed in Muren et al. (1986) and Hyrtl (1845), as well as direct measurements from serial sections of one temporal bone, were used in calculating the values of humans, *Pongo pygmaeus*, and *Pan troglodytes*, respectively.

The dimensions of the semicircular canals and the cochlea were considered relative to both the basicranial size and body size of the species. The former was quantified by the average of basion-nasion length and bicaudicular breadth taken from the skulls to the nearest millimeter and the latter by body mass as given in Smith and Jungers (1997). The basicranial size correlates well with the body mass values (correlation coefficient $r_s = 0.957$), despite the fact that the former were taken from the specimens used in this study and the latter were obtained from the literature. Both give similar results in the analyses of labyrinthine dimensions, and the results presented here are those using body mass because they allow inclusion of canal sizes obtained from the literature. Body masses of nonprimate mammals were taken from Silva and Downing (1995).

Two linear measurements were taken to calculate the sagittal labyrinthine index, which expresses the percentage of the posterior semicircular canal that is located inferiorly to the level of the lateral semicircular canal (Table 2; SLIs and SLIi, Fig. 1b). This index has previously been used in comparative studies (Spoor and Zonneveld, 1995; Hublin et al., 1996).

Angles were taken to quantify the spatial orientation of labyrinthine structures in relation to each other and in relation to aspects of the cranium. All orientations are

defined in the transverse or sagittal plane (Fig. 1c,d), and angles calculated between two such orientations are therefore projected onto either of these planes. Angles are indicated by the abbreviations of the two orientations on which they are based, separated by the < symbol. For example, CCR < LSCm is the angle between the common crus and the lateral canal in the sagittal plane (Fig. 1d).

The orientations of the lateral semicircular canal in the sagittal plane (LSCm, Fig. 1d) and of the vertical canals in the transverse plane (ASCm and PSCm, Fig. 1c) were measured at the widest part of their arc. These measurements provide two-dimensional representations of the functionally important planar orientations of the canals. Interspecifically they were found to be the most stable parts of the primate labyrinth, and they are therefore used as reference orientations in comparisons of other, more diverse aspects of labyrinthine shape. By taking the line bisecting the anteriorly facing angle between the orientations of the anterior and posterior canals, we combine the two into a single reference orientation in the transverse plane (VSC based on ASCm and PSCm, Fig. 1c).

The torsion of the anterior and posterior canals is quantified as the difference between the orientations of their superiormost and inferiormost parts (ASCs-ASCI and PSCs-PSCI, Fig. 1c) and that of the lateral canal as the difference between orientations of the lateralmost part and at the greatest arc width (LSCI-LSCm, Fig. 1d). In *Saimiri*, *Propithecus*, and *Indri*, one or more of these measurements could not be taken owing to the limitations of the spatial resolution of the CT image. In these cases, the small canal lumen could not be distinguished from the endocranial cavity because the two are separated by a very thin layer of bone only (owing to partial volume averaging). The orientation of the basal turn of the cochlea is measured at its greatest width both in the transverse and sagittal planes (COt, Fig. 1c; COs, Fig. 1d). Finally, four characters are quantified that in previous studies have been associated with aspects of overall basicranial architecture. These are the orientations of the common crus (CCR, Fig. 1d) and

the ampullar line (APA, Fig. 1d), first described in Werner (1933), the orientation of the vestibulo-cochlear line (VC, Fig. 1d), describing the position of the cochlea relative to the vestibular parts of the labyrinth and described in Delattre and Fenart (1961), and the orientation of the axis of symmetry of the lateral canal (LSCt, Fig. 1c), described in Spoor and Zonneveld (1994a).

To examine the labyrinth in relation to cranial morphology, we recorded the orientation of the midsagittal plane in transverse CT scans. Moreover, midsagittal scans were used to measure the orientations of the lines basion to nasion (ba-na), sella to foramen caecum (s-fc), basion to sella (ba-s), and opisthion to basion (o-ba), representing the overall midline basicranial orientation and the orientations of the anterior cranial base, the basioccipital, and the foramen magnum, respectively (Fig. 2a). The cross-sectional orientation of the posterior surface of the petrous pyramid was measured both from a parasagittal CT scan and a transverse CT scan at the level of the labyrinth (Ppp in Fig. 2 and PPip in Fig. 2b, respectively). The midsagittal measurements were not taken from the soft-tissue specimen of *M. fascicularis*, as its basioccipital synchondrosis was not fully fused.

F-tests and *t*-tests were used to investigate the statistical significance of differences between variances and between means. In those comparisons where the F-test indicated dissimilarity of the variances, the alternative for the *t*-test, given by Sokal and Rohlf (1969), was used. Both angles and indices are based on two variables and therefore do not necessarily show a normal distribution in a population. However, the *t*-test is considered sufficiently robust in this respect to justify its use here (G.N. Van Vark, personal communication).

Interspecific morphological relationships between the labyrinth, basicranial angles, and body mass were investigated by calculating Spearman rank correlation coefficients (r_s) using the mean values for primate species represented by multiple specimens. This nonparametric method was used because species means of measurements obtained for an arbitrary selection of species are unlikely to be normally distributed. In practice, it

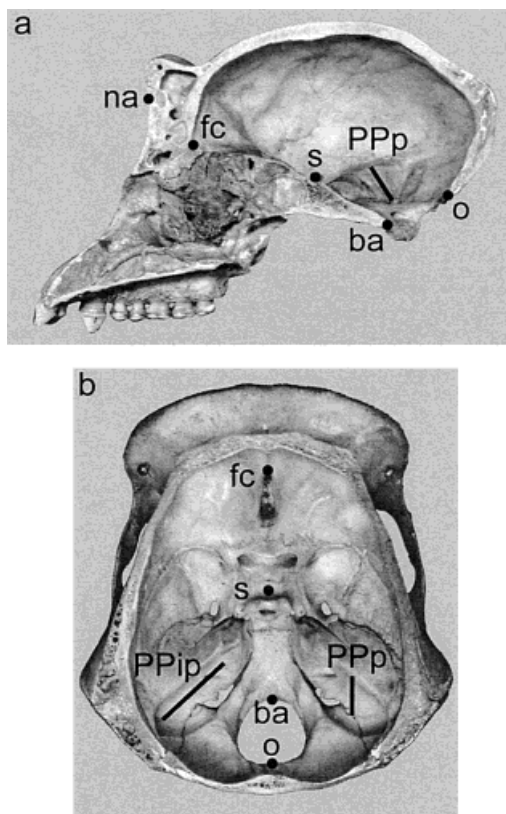


Fig. 2. **a:** Medial view of a midsagittally sectioned cranium of *Pan troglodytes* showing the landmarks opisthion (o), basion (ba), sella (s), foramen caecum (fc), and nasion (na) as well as the orientation of the posterior petrosal surface (PPp). **b:** Superior view of the internal surface of the cranial base of *P. troglodytes* showing the orientation of the posterior petrosal surface (PPip) and the landmarks given in panel a.

was found that the results differ only marginally from those obtained by using the Pearson product-moment correlation coefficient, which assumes normality. In all statistical tests, the null hypothesis was rejected at $P < 0.05$. Where helpful in the interpretation of bivariate plots, reduced major axis regression lines are given.

DESCRIPTIONS AND COMPARISONS

A selection of transverse CT scans of primate temporal bones at the level of the lateral semicircular canal is given in Figure 3. Reconstructions of the superior and lateral aspects of the bony labyrinths of humans, the great apes, and a selection of other primates are shown in Figures 4 and

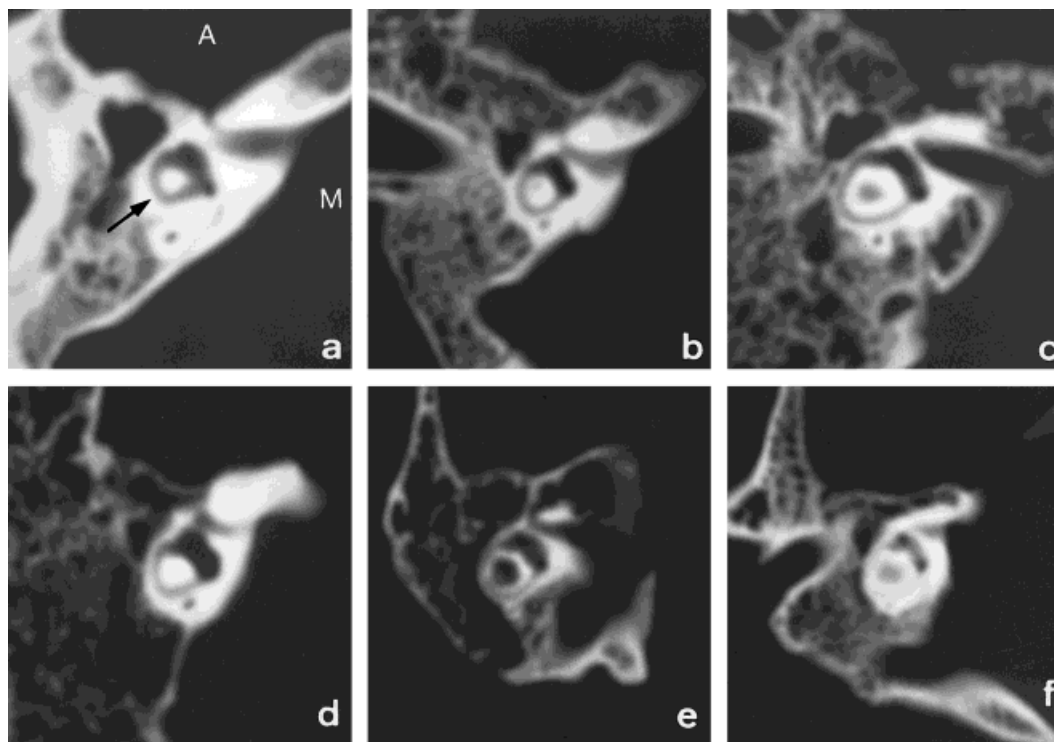


Fig. 3. Transverse CT scans of primate temporal bones at the level of the left lateral semicircular canal (arrow in panel a). **a:** *Homo sapiens*. A, anterior; M, medial. **b:** *Pan paniscus*. **c:** *Gorilla gorilla*. **d:** *Pongo pygmaeus*. **e:** *Hylobates syndactylus*. **f:** *Papio ursinus*.

5, respectively. When in the following sections the semicircular canals or the cochlea are described as large or small, this specifically refers to the arc size of the canals and the basal turn size of the cochlea as expressed by their radius of curvature. When the lumen size of these structures is implied, this is explicitly stated.

Semicircular canals

The radii of curvature of the arcs of the semicircular canals are given in Table 3. The statistical significance of the difference between the means of the CT-based human sample and the great ape species is indicated. The human anterior semicircular canal is larger than that of the great apes. Among the other species, this canal is particularly large in *Propithecus* and *Ateles*. The posterior canal radius of humans equals that of *Gorilla* and is larger than that of the other primates. The human lateral semicircular canal is smaller than that of the great

apes other than *Pan paniscus* and similar in size to that in many other species. This pattern of semicircular canal sizes can be summarized by calculating their relative radii of curvature, giving the radius of each canal as a percentage of the sum of the three (%R, Table 3). These values demonstrate the relatively large vertical canals and small lateral canal in humans when compared with the great apes and most other primates. The atelines and *Nycticebus* show a characteristic pattern of a relatively small lateral canal and a relatively large anterior canal. Correlation coefficients calculated between the canal radii are statistically highly significant ($P < 0.001$), with that between the anterior and posterior canals ($r_s = 0.836$) somewhat higher than those between the lateral and anterior or posterior canals ($r_s = 0.645$ and 0.710 , respectively).

Bivariate double logarithmic plots demonstrate the positive correlation between the radii of curvature of the semicircular canals

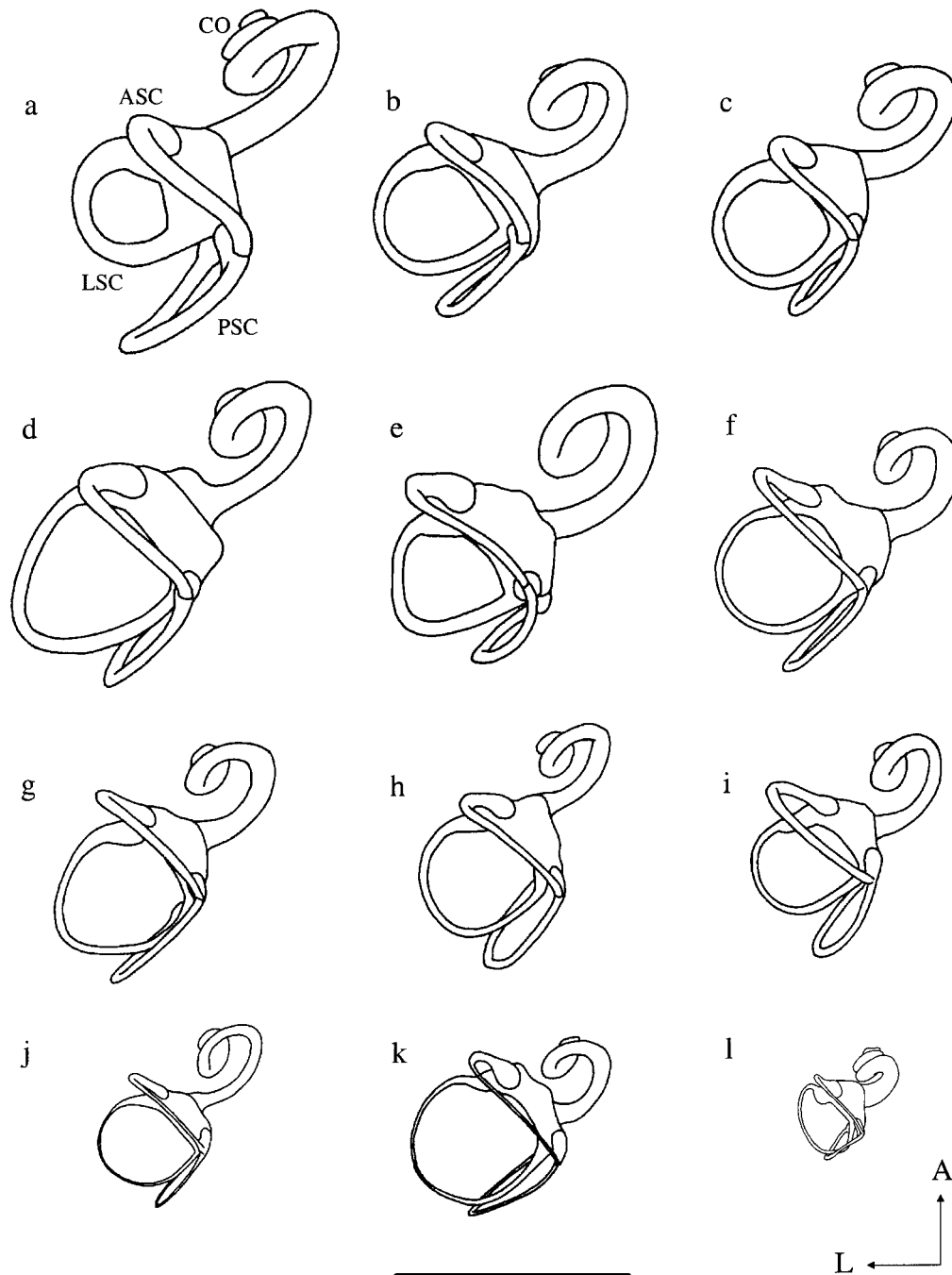


Fig. 4. Superior aspect of the left bony labyrinths of primates reconstructed from transverse CT scans. ASC, PSC, LSC, anterior, posterior, and lateral semicircular canals, respectively; CO, cochlea. Labyrinths aligned according to their orientation to the midsagittal plane. A, anterior; L, lateral. Scale bar is 10 mm. **a:** *Homo*

sapiens. **b:** *Pan troglodytes*. **c:** *Pan paniscus*. **d:** *Gorilla gorilla*. **e:** *Pongo pygmaeus*. **f:** *Hylobates syndactylus*. **g:** *Papio ursinus*. **h:** *Macaca fascicularis*. **i:** *Lagothrix lagotricha*. **j:** *Saimiri sciureus*. **k:** *Propithecus diadema*. **l:** *Microcebus rufus*.

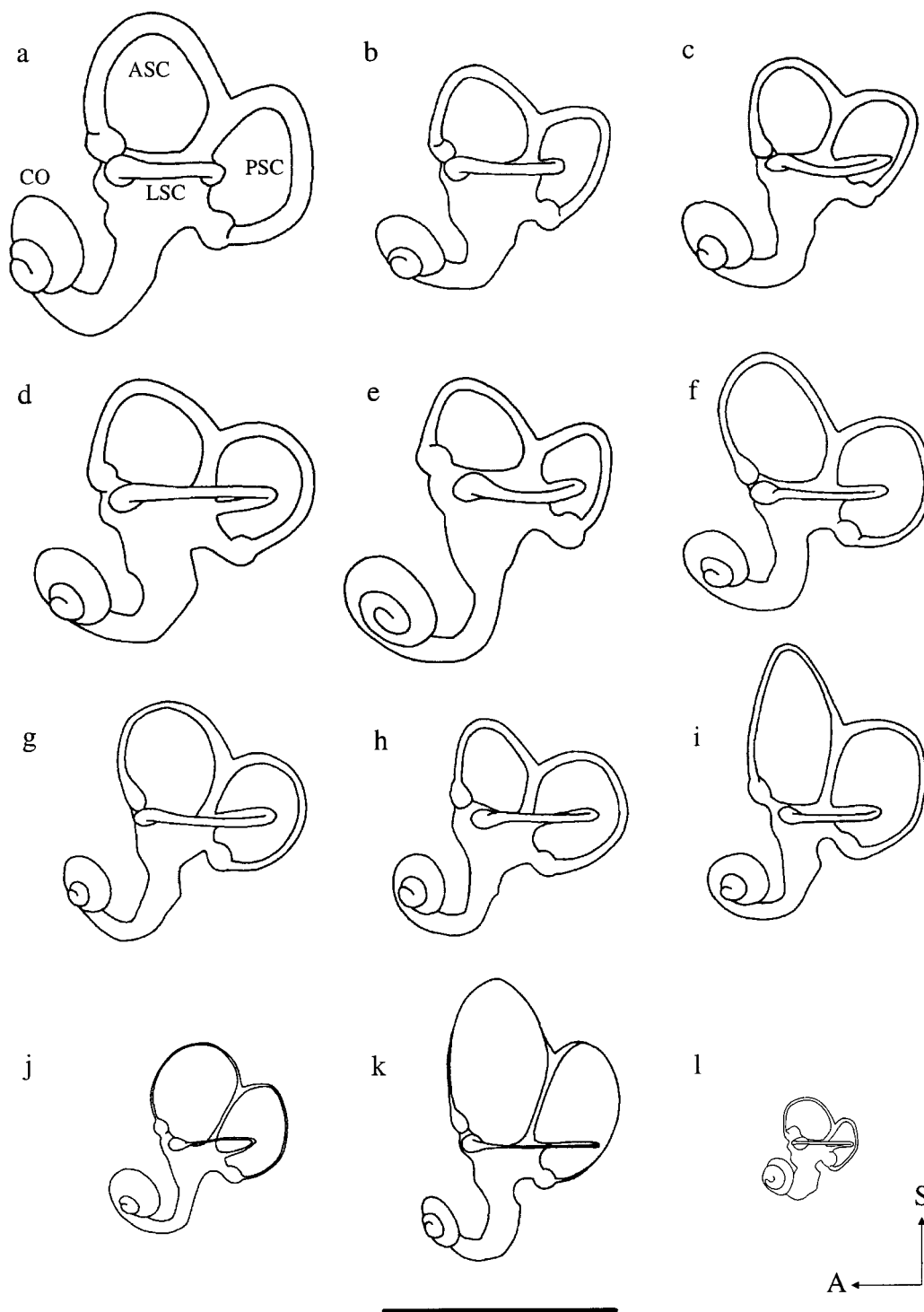


Fig. 5. Lateral view of the left bony labyrinths of primates reconstructed from sagittal CT scans. Species as in Fig. 4. ASC, PSC, LSC, anterior, posterior, and lateral semicircular canals, respectively; CO, cochlea. Labyrinths aligned according to the orientation of the lateral semicircular canal (LSCm). A, anterior; S, superior. Scale bar is 10 mm.

TABLE 3. Radii of curvature to the center of the lumen (R) of the semicircular canals (ASC, PSC, LSC) given in millimeters and the relative radii of the semicircular canals in per cent (%R; sum of the three radii is 100%)¹

	ASC-R		PSC-R		LSC-R		ASC %R	PSC %R	LSC %R
	Mean	SD	Mean	SD	Mean	SD			
<i>Homo sapiens</i> (CT)	3.2	0.24	3.1	0.30	2.3	0.21	37	37	26
<i>Homo sapiens</i> (all)	3.3		3.1		2.2		38	36	26
<i>Pan troglodytes</i>	2.7	0.20	2.8	0.24	2.4	0.24	34	35	31
<i>Pan paniscus</i>	2.6	0.19	2.5	0.16	2.4	0.18	35	34	32
<i>Gorilla gorilla</i>	2.9	0.16	3.1	0.27	3.1	0.23	32	34	34
<i>Pongo pygmaeus</i>	2.7	0.23	2.6	0.27	2.4	0.10	35	34	31
<i>Hylobates syndactylus</i>	3.0	0.04	2.8	0.07	2.6	0.11	36	33	31
<i>Hylobates lar</i>	2.7		2.5		2.2		37	33	30
<i>Hylobates moloch</i>	2.7		2.5		2.5		35	32	33
<i>Hylobates pileatus</i>	2.7		2.6		2.5		34	33	32
<i>Macaca fascicularis</i> (CT)	2.4	0.16	2.2	0.17	2.2	0.18	35	33	32
<i>Macaca fascicularis</i> (all)	2.4		2.3		2.2		35	33	32
<i>Macaca mulatta</i>	2.7		2.5		2.4		36	33	32
<i>Macaca nemestrina</i>	2.7		2.7		2.1		36	36	28
<i>Macaca nigra</i>	2.4		2.1		1.8		38	33	29
<i>Macaca tonkeana</i>	2.6		2.4		2.4		35	33	32
<i>Macaca cyclopis</i>	2.5		2.5		2.3		34	34	32
<i>Macaca fuscata</i>	2.6		2.7		2.3		35	35	30
<i>Papio ursinus</i>	2.9		2.6		2.7		35	32	33
<i>Papio cynocephalus</i>	2.8		2.6		2.6		35	33	33
<i>Papio hamadryas</i>	2.9		2.7		2.6		35	33	32
<i>Theropithecus gelada</i>	2.9		2.7		2.4		36	33	30
<i>Mandrillus sphinx</i>	2.8		2.8		2.6		34	34	32
<i>Cercopithecus aethiops</i>	2.5		2.6		2.3		34	35	31
<i>Cercopithecus nictitans</i>	2.3		2.2		2.3		34	32	34
<i>Cercopithecus mona</i>	2.3		2.3		2.3		34	33	33
<i>Colobus guereza</i>	2.9		2.6		2.4		37	33	30
<i>Presbytis entellus</i>	2.5		2.4		2.3		35	33	32
<i>Nasalis larvatus</i>	3.0		2.6		2.7		36	31	33
<i>Callithrix jacchus</i>	1.5		1.6		1.4		33	36	31
<i>Cebus apella</i>	2.4		2.2		2.0		36	33	30
<i>Saimiri sciureus</i>	2.1		1.8		1.7		38	31	31
<i>Aotus trivirgatus</i>	2.3		2.0		1.8		38	32	30
<i>Lagothrix lagothricha</i>	3.1		2.6		2.0		41	34	25
<i>Alouatta seniculus</i>	2.9	0.18	2.4	0.13	2.0	0.37	39	33	28
<i>Ateles geoffroyi</i>	3.3		2.8		2.1		41	34	25
<i>Tarsius bancanus</i>	1.9		1.7		1.8		35	32	33
<i>Propithecus diadema</i>	3.2		2.8		2.5		38	33	29
<i>Indri indri</i>	2.8		2.2		2.2		39	30	31
<i>Lemur catta</i>	2.3		1.9		1.9		38	31	31
<i>Eulemur macaco</i>	2.4		2.4		2.0		36	35	30
<i>Eulemur mongoz</i>	2.4		2.5		2.0		35	36	30
<i>Microcebus rufus</i>	1.2		1.0		1.1		35	32	33
<i>Nycticebus coucang</i>	2.0		1.6		1.3		40	33	27
<i>Homo sapiens</i> (CT) compared with									
<i>Pan troglodytes</i>	***>		***>		*<				
<i>Pan paniscus</i>	***>		***>						
<i>Gorilla gorilla</i>	**>				***<				
<i>Pongo pygmaeus</i>	***>		***>		**<				

¹ The standard deviation (SD) is available only for the CT sample or the CT sample plus one published specimen. The statistical significance of the difference between the means of humans and the great apes is $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***). If the human value is larger than the great ape value, this is indicated by >; if it is smaller, this is indicated by <.

and body mass (Fig. 6). Correlation coefficients (r_s) of 0.754, 0.794, and 0.734 for the anterior, posterior, and lateral canal, respectively, are statistically significant at $P < 0.001$. The great apes fall below and more or less parallel with the overall trend among other primates for all three canals. Hence, with body mass taken into account, the canals of the great apes are consistently

smaller than those of most other primate species. In contrast, hylobatids are among the species with relatively large canals. The anterior and posterior canals of humans are larger than those of the great apes but consistent with the trend in most other species (Fig. 6a,b). The lateral canal of humans is somewhat smaller than in the great apes and considerably smaller than in most

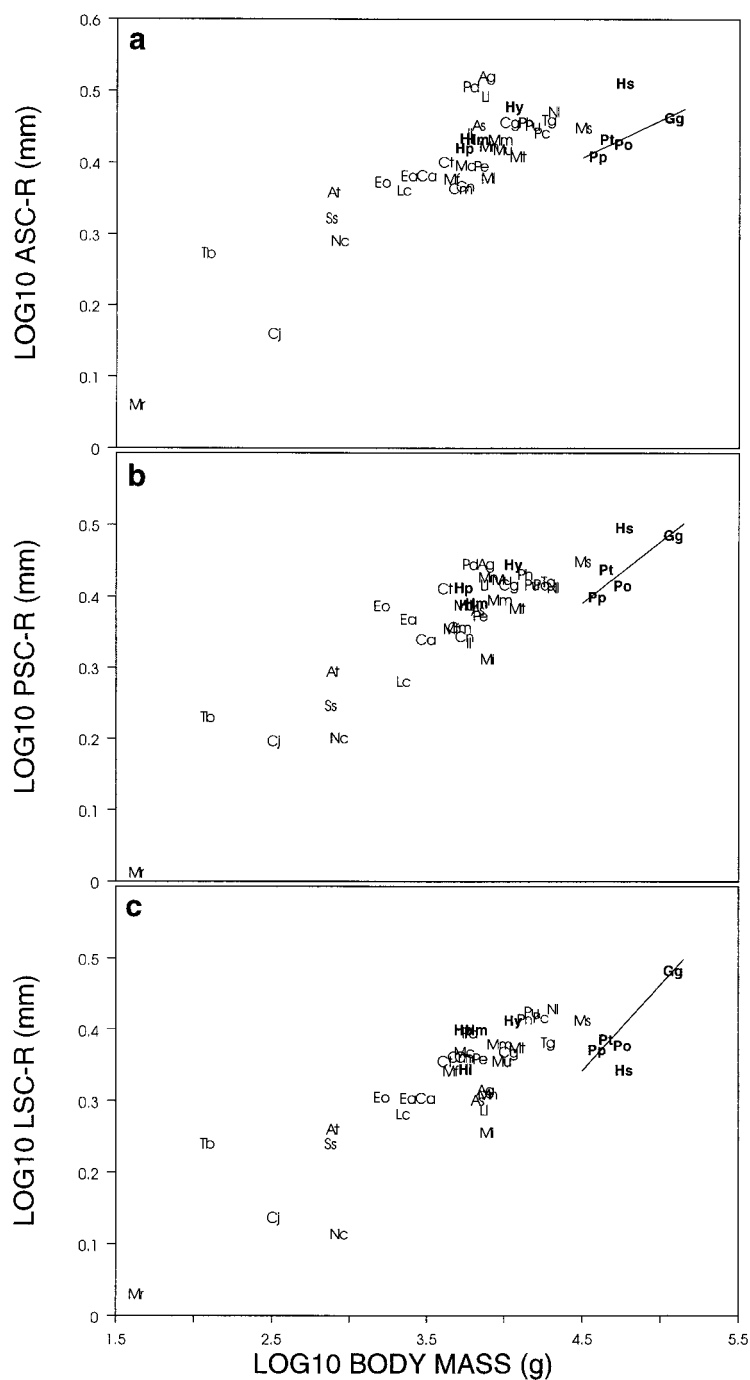
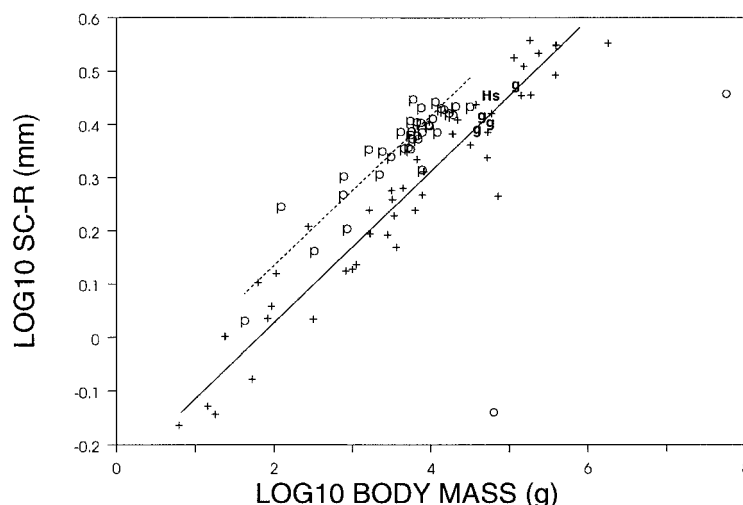


Fig. 6. Bivariate double logarithmic plots between body mass and the radii of curvature to the center of the lumen of (a) the anterior semicircular canal (ASC-R), (b) the posterior canal (PSC-R), and (c) the lateral canal (LSC-R). Species codes are listed in Table 1, and those of the hominoids are given in bold. The reduced major axis regressions for the great ape species are indicated.

other species (Fig. 6c). Among the nonhominoids, the anterior canal is particularly large in *Ateles*, *Lagothrix*, and *Propithecus* (Fig. 6a). The size of this canal in the smallest

species is difficult to interpret, other than that it is clearly larger in *Tarsius* than in *Callithrix* and *Microcebus*. The posterior and lateral canals of *Macaca nigra* are small

Fig. 7. Bivariate double logarithmic plot between body mass and the mean of the radii of curvature to the center of the anterior, posterior, and lateral semicircular canals (SC-R). g, great apes; Hs, *Homo sapiens*; o, the common porpoise *Phocoena phocoena* and the right whale *Eubalaena glacialis*; p, other primates; +, 43 other non-primate mammals. The solid line is the reduced major axis regression for the mammals other than the primates and the two cetaceans ($r_s = 0.962$, slope = 0.142, intercept = -0.256), the dashed line that for the primates other than the great apes and *H. sapiens* ($r_s = 0.826$, slope = 0.141, intercept = -0.146).



relative to other cercopithecoids, and the lateral canal is particularly large in *Tarsius* and small in *Nycticebus* (Fig. 6b,c). *Mandrillus* tends to take a position halfway between the great apes and cercopithecoids, in particular for the anterior canal (Fig. 6a). It should be noted that body masses reported for males of this species vary widely, from 31.6 kg (Smith and Jungers, 1997), used here, to 26.9 kg (Fleagle, 1988), previously used in Spoor et al. (1994), to 21.5 kg (R. Martin, personal communication), used in Spoor et al. (1996). When the last value is taken, *Mandrillus* falls with the other cercopithecoids.

To examine how primate semicircular canal size compares with the general trend among mammals, Figure 7 plots the mean of the anterior, posterior, and lateral canal radii against body mass for the primate sample and 45 other mammalian species, ranging from the pipistrelle and the house mouse to the Asiatic elephant and the right whale. The canal radius and body mass are well correlated among these mammals, with the exception of the two cetaceans in the sample, which have greatly reduced canals. The great apes closely follow the general mammalian trend, as indicated by the reduced major axis. The regression for the other primates falls above and parallel with the mammalian trend, and as a group these primates are thus characterized by relatively large canals for their body mass. In

TABLE 4. Radii of curvature to the outer wall (R') of the semicircular canals (ASC, PSC, LSC) given in millimeters

	ASC-R'	PSC-R'	LSC-R'
<i>Homo sapiens</i>	3.7	3.8	2.9
<i>Pan troglodytes</i>	3.1	3.2	2.8
<i>Gorilla gorilla</i>	3.3	3.6	3.5
<i>Pongo pygmaeus</i>	3.1	3.3	2.9
<i>Hylobates lar</i>	2.9	2.7	2.5
<i>Macaca fascicularis</i>	2.6	2.6	2.5
<i>Macaca nemestrina</i>	2.8	2.9	2.2
<i>Macaca nigra</i>	2.7	2.4	2.1
<i>Macaca tonkeana</i>	2.8	2.7	2.6
<i>Macaca cyclopis</i>	2.7	2.7	2.6
<i>Macaca fuscata</i>	2.8	3.0	2.5
<i>Papio cynocephalus</i>	3.0	3.0	2.9
<i>Papio hamadryas</i>	3.1	3.0	2.8
<i>Cercopithecus aethiops</i>	2.8	3.1	2.7
<i>Cercopithecus nictitans</i>	2.7	2.6	2.6
<i>Cercopithecus mona</i>	2.5	2.5	2.5
<i>Callithrix jacchus</i>	1.6	1.8	1.6
<i>Saimiri sciureus</i>	2.3	2.0	2.1
<i>Aotus trivirgatus</i>	2.5	2.2	2.0
<i>Alouatta seniculus</i>	3.0	2.7	2.2
<i>Ateles geoffroyi</i>	3.6	3.1	2.5
<i>Tarsius bancanus</i>	2.1	1.9	1.9
<i>Lemur catta</i>	2.4	2.1	2.0
<i>Eulemur macaco</i>	2.6	2.6	2.2
<i>Eulemur mongoz</i>	2.5	2.7	2.2
<i>Nycticebus coucang</i>	2.1	1.8	1.5

this graph, the difference between humans and the great apes is small because the human value averages the larger anterior and posterior canals and the smaller lateral canal.

Table 4 lists the radii of curvature of the semicircular canals measured to the outer canal wall instead of the center of the lumen. Correlation coefficients (r_s) with body masses

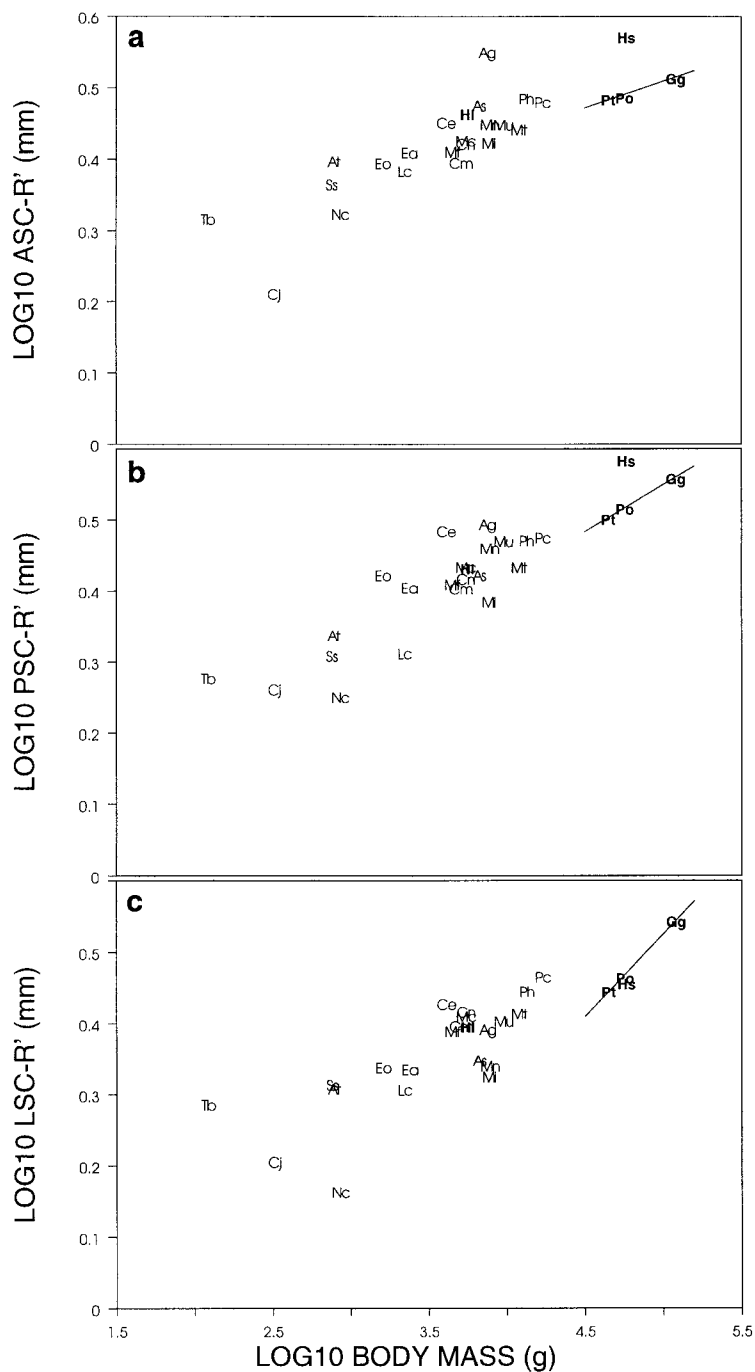


Fig. 8. Bivariate double logarithmic plots between body mass and the radii of curvature to the outermost wall of (a) the anterior semicircular canal (ASC-R'), (b) the posterior canal (PSC-R'), and (c) the lateral canal (LSC-R'). Species codes are listed in Table 1, and those of the hominoids are given in bold. The reduced major axis regressions for the great ape species are indicated.

of 0.895, 0.856, and 0.839 for the anterior, posterior, and lateral canal, respectively, are statistically significant at $P < 0.001$. Plots of these relationships (Fig. 8) reveal less differ-

ence between the great apes and other primates than seen for the radii to the lumen's center (Fig. 6). The radii of the anterior and posterior canals are larger in humans than

TABLE 5. The shape indices ($h/w \times 100$) and torsions (tor) of the semicircular canals (ASC, PSC, LSC)¹

	ASC h/w		PSC h/w		LSC h/w		ASCtor ²		PSCtor ³		LSCtor ⁴	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Homo sapiens</i>	87	4.6	107	7.6	89	7.0	16	5.3	-9	4.5	4	4.1
<i>Pan troglodytes</i>	80	4.5	102	10.5	92	5.1	13	4.9	7	3.9	2	1.9
<i>Pan paniscus</i>	81	3.8	93	5.8	87	6.1	8	5.5	6	2.9	3	0.7
<i>Gorilla gorilla</i>	71	5.9	109	4.8	101	6.2	15	3.4	2	1.1	4	5.5
<i>Pongo pygmaeus</i>	73	8.8	104	7.2	89	7.7	20	4.6	8	5.1	7	5.3
<i>Hylobates syndactylus</i>	86	1.9	106	7.9	96	2.5	2	0.6	-8	0.5	2	0.9
<i>Hylobates moloch</i>	91		106		94		18		1		10	
<i>Hylobates pileatus</i>	80		117		94		9		7		8	
<i>Macaca fascicularis</i>	87	6.1	95	3.6	92	7.0	19	6.0	2	1.8	2	1.4
<i>Papio ursinus</i>	84		110		106		9		-3		4	
<i>Theropithecus gelada</i>	93		112		94		13		-9		3	
<i>Mandrillus sphinx</i>	85		109		96		11		-3		4	
<i>Colobus guereza</i>	95		102		92		-1		0		1	
<i>Presbytis entellus</i>	92		94		88		12		-1		6	
<i>Nasalis larvatus</i>	98		112		93		15		-5		6	
<i>Cebus apella</i>	94		91		76		15		-12		1	
<i>Saimiri sciureus</i>	100		93		78		1		—		—	
<i>Lagothrix lagothricha</i>	127		84		105		11		4		4	
<i>Alouatta seniculus</i>	92		90		82		13		-10		7	
<i>Propithecus diadema</i>	119		87		92		—		—		—	
<i>Indri indri</i>	88		98		93		2		1		—	
<i>Microcebus rufus</i>	66		86		58		11		-11		3	
<i>Homo sapiens</i> (CT) compared with												
<i>Pan troglodytes</i>	***>								***<			
<i>Pan paniscus</i>	***>		***>				***>		***<			
<i>Gorilla gorilla</i>	***>				***>				***<			
<i>Pongo pygmaeus</i>	***>								***<			

¹ Statistical significance between humans and the great apes as indicated in the caption of Table 3.² Positive when ASCs is more coronally oriented than ASCi.³ Positive when PSCs is more sagittally oriented than PSCi.⁴ LSCi is more inclined than LSCm.

in the great apes, more so than when measured to the center of the lumen, whereas the lateral canal radii are similar in both (Fig. 8). Dissimilarities between the plots based on the two alternative radius definitions are caused by the diversity of lumen size among primates, which can be seen but not accurately measured in the CT scans and the reconstructions (Figs. 3–5).

The height-to-width proportions of the canal arcs are listed in Table 5 for the species in the CT sample. The proportions of the human posterior and lateral semicircular canals correspond to those in most great ape species as well as to those in many of the other primates. Among the hominoids, the posterior canal of *P. paniscus* stands out by having a height which is less than its width and the lateral canal of *Gorilla* by having a height which is greater than its width (Figs. 3c, 4d). The arc of the anterior canal is relatively low in the great apes and *Microcebus* when compared with humans and other

primates, whereas that of *Lagothrix* and *Propithecus* is particularly high (Fig. 5).

The semicircular canals also show an interspecific diversity of shapes that is not captured by their height and width measurements (Figs. 3, 4). For example, the lateral semicircular canal is round or slightly oval in most species, including humans, *Pan*, and *Hylobates*, whereas it is oval and parabolically shaped in *Gorilla*, *Papio*, *Theropithecus*, and *Mandrillus* (Fig. 4). In *Microcebus* it has a strongly asymmetrical, medioposteriorly skewed shape (Fig. 4l), and in *Pongo* it has a characteristically straight segment bordering the tympanic cavity between the ampulla and the vertex (Figs. 3d, 4e). *Pongo* is also characterized by a very short common crus with a wide lumen (Fig. 5e). The posterior canal of the great apes is characterized by a more inclined orientation of its inferior limb than occurs in other species (Fig. 5b–e).

Table 6 lists angles describing the orientation of the semicircular canals within the

TABLE 6. Angles in degrees describing the semicircular canal orientations in the cranium¹

	ASCm < SG		PSCm < SG		LSCm < ba-na		LSCm < s-fc		LSCm < ba-s		LSCm < o-ba		LSCm < PPp	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Homo sapiens</i>	36	4.9	139	5.4	10	5.4	-3	5.9	39	6.1	-10	7.9	62	7.9
<i>Pan troglodytes</i>	37	2.4	139	3.5	6	4.0	-7	3.8	19	5.1	-39	5.1	34	8.9
<i>Pan paniscus</i>	38	5.5	142	6.0	10	5.4	-9	7.8	23	4.5	-37	8.1	36	7.1
<i>Gorilla gorilla</i>	39	3.5	139	7.3	10	4.3	-10	7.5	16	5.0	-46	5.7	37	10.2
<i>Pongo pygmaeus</i>	42	3.5	147	5.6	2	8.3	-16	11.2	5	9.2	-53	15.5	23	8.1
<i>Hylobates syndactylus</i>	41	0.1	143	2.0	-1	1.3	-5	0.1	2	0.1	-52	4.5	20	3.2
<i>Hylobates moloch</i>	34		139		3		-1		10		-47		32	
<i>Hylobates pileatus</i>	38		142		-5		-5		9		-49		13	
<i>Macaca fascicularis</i>	42	4.2	143	4.1	3	4.0	-2	2.3	5	1.8	-43	2.3	38	8.4
<i>Papio ursinus</i>	41		142		20		7		34		-31		43	
<i>Theropithecus gelada</i>	45		146		17		11		35		-33		56	
<i>Mandrillus sphinx</i>	34		135		13		0		18		-40		48	
<i>Colobus guereza</i>	39		143		2		2		9		-54		56	
<i>Presbytis entellus</i>	37		148		12		8		22		-42		56	
<i>Nasalis larvatus</i>	40		143		5		1		12		-39		48	
<i>Cebus apella</i>	35		139		5		2		14		-49		57	
<i>Saimiri sciureus</i>	41		145		5		1		12		-44		28	
<i>Lagothrix lagothricha</i>	49		152		-5		-7		-2		-52		26	
<i>Alouatta seniculus</i>	44		152		-15		-15		-20		-85		22	
<i>Propithecus diadema</i>	43		135		-7		3		-3		-70		34	
<i>Indri indri</i>	36		134		-6		-8		0		-64		28	
<i>Microcebus rufus</i>	41		134		3		-3		-1		-59		29	
<i>Homo sapiens</i> compared with														
<i>Pan troglodytes</i>									***>		***>		***>	
<i>Pan paniscus</i>									***>		***>		***>	
<i>Gorilla gorilla</i>								*>	***>		***>		***>	
<i>Pongo pygmaeus</i>	**<		**<		**>		***>		***>		**>		***>	

¹ Explanation of the measurement codes and symbols in Fig. 1 and Tables 2 and 3. Angles of ASCm and PSCm open anteriorly, the others opening anterosuperiorly to LSCm have positive values, those opening anteroinferiorly to LSCm negative ones.

cranium. The anterior and posterior canal orientations relative to the midsagittal plane are not significantly different in humans and the African apes (ASCm < SG and PSCm < SG, Table 6). Compared with these species, the anterior and posterior canals of *Pongo* are more coronally and sagittally oriented, respectively, a morphology seen to a much greater degree in the two ateline specimens.

The lateral canal orientation relative to the external basicranial line is similar in humans and the African apes and somewhat smaller in *Pongo*, indicating a slightly more inclined canal (LSCm < ba-na, Table 6). Relative to the anterior cranial base, the lateral canal orientation is not significantly different in humans and *Pan*, whereas it is more inclined in *Gorilla* and *Pongo* (LSCm < s-fc, Table 6). Among the other species, the two angles have both smaller and larger values, with *Papio* and *Theropithecus* showing a particularly declined lateral canal and *Alouatta* a clearly inclined canal.

Angles between the human lateral canal and three orientations associated with the posterior cranial fossa consistently differ from those in other primates, expressing a more inclined basioccipital and posterior petrosal surface as well as a less declined foramen magnum relative to the canal orientation (LSCm < ba-s, LSCm < PPp, and LSCm < o-ba, respectively, in Table 6). Non-hominoid species, such as *Theropithecus* and *Papio*, are closer to humans than the great apes for all three angles.

With respect to semicircular canal torsion, the only consistent differences between humans and the great apes occur for the posterior canal (PSCtor, Table 5). In humans, the superior limb is more coronally oriented than the inferior limb (Fig. 4a), giving negative torsion values, whereas the great apes show a reverse configuration (Fig. 4b-e). In other species, the degree of posterior canal torsion is variable but more similar to humans than to the great apes. Torsion of the anterior and lateral canals is variable in the sample, without a clear pattern of differ-

TABLE 7. Angles in degrees and index (SLI) in per cent of the semicircular canals¹

	AScM < PSCm		LSCt < VSC		CCR < LSCm		APA < LSCm		SLI	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Homo sapiens</i>	104	5.2	112	5.0	121	4.0	41	4.7	51	7.1
<i>Pan troglodytes</i>	102	3.9	130	3.9	106	1.6	35	2.2	44	4.6
<i>Pan paniscus</i>	104	4.5	125	1.9	111	2.6	31	1.8	36	3.4
<i>Gorilla gorilla</i>	101	9.2	127	3.5	106	3.4	33	2.5	48	5.7
<i>Pongo pygmaeus</i>	107	5.2	126	2.1	104	4.1	27	5.6	35	10.0
<i>Hylobates syndactylus</i>	103	1.9	126	0.1	111	8.3	30	3.2	42	5.3
<i>Hylobates moloch</i>	105		124		111		35		48	
<i>Hylobates pileatus</i>	104		119		112		31		44	
<i>Macaca fascicularis</i>	101	1.6	124	0.9	101	1.1	35	1.6	43	7.2
<i>Papio ursinus</i>	101		129		115		38		46	
<i>Theropithecus gelada</i>	101		126		119		45		56	
<i>Mandrillus sphinx</i>	102		134		118		40		51	
<i>Colobus guereza</i>	105		138		118		34		48	
<i>Presbytis entellus</i>	110		127		114		41		56	
<i>Nasalis larvatus</i>	103		125		117		43		62	
<i>Cebus apella</i>	104		132		110		37		46	
<i>Saimiri sciureus</i>	103		124		108		33		39	
<i>Lagothrix lagothricha</i>	103		111		105		31		31	
<i>Alouatta seniculus</i>	108		111		109		26		27	
<i>Propithecus diadema</i>	93		123		107		34		26	
<i>Indri indri</i>	98		126		105		30		31	
<i>Microcebus rufus</i>	93		127		121		32		52	
<i>Homo sapiens</i> compared with										
<i>Pan troglodytes</i>			***<		***>		**>		*>	
<i>Pan paniscus</i>			***<		***>		***>		***>	
<i>Gorilla gorilla</i>			***<		***>		***>			
<i>Pongo pygmaeus</i>			***<		***>		***>		***>	

¹ Explanation of the measurement codes and symbols in Fig. 1 and Tables 2 and 3. The first two angles open laterally, the other two anterosuperiorly.

ences (AScM and LSCM, Table 5; Figs. 4, 5).

Table 7 gives four angles and an index describing the spatial relationship between aspects of the three semicircular canals. The angle between the anterior and posterior canal is remarkably constant among the anthropoids in the sample, with somewhat smaller values seen in the three prosimians (AScM<PSCM, Table 7). It is not significantly different in humans and the great apes. In contrast, the vertex of the lateral semicircular canal (the point furthest from the vestibule) is directed more laterally in humans than in other primates (Fig. 4). The axis of symmetry of the lateral canal is therefore more coronally oriented, as is shown by its angle relative to the vertical canals (LSCt < VSC, Table 7). Human-like values for this angle only occur in *Lagothrix* and *Alouatta*, owing to the unusual vertical canal orientations in these species (Table 6). When calculated relative to the midsagittal plane, the axis of the human lateral canal differs from that of all other species, includ-

ing the two atelines (LSCt < SG: humans, 110°; other primates, 119–139°).

Relative to the lateral canal orientation, the common crus of the human labyrinth is more posteriorly tilted, and the ampullar line, connecting the anterior and posterior ampullae, is more inclined than in other hominoids and some of the other primates (Fig. 5; CCR < LSCM and APA < LSCM, Table 7). In humans, the plane of the lateral canal divides the arc of the posterior canal in about equal halves (Fig. 5a), giving a sagittal labyrinthine index of 51 (SLI, Table 7). In the great apes other than *Gorilla* as well as in some of the other species, the lateral canal divides the arc of the posterior canal in a larger superior and a smaller inferior part, giving index values significantly lower than 50. Others, most prominently the specimen of *Nasalis*, show values of over 50.

Cochlea

The basal turn of the human cochlea is larger than that of other species and tends to be relatively wide (CO-R and COh/w, Table

TABLE 8. Linear dimensions and angles of the cochlea¹

	CO-R		CO h/w		COt < VSC		VC < LSCm		COs < LSCm	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Homo sapiens</i>	2.3	0.13	136	8.6	116	4.9	151	6.1	59	5.1
<i>Pan troglodytes</i>	2.0	0.20	151	12.2	120	9.5	142	5.9	39	6.2
<i>Pan paniscus</i>	2.0	0.17	145	9.7	118	11.1	141	3.2	35	2.3
<i>Gorilla gorilla</i>	2.1	0.24	143	12.3	116	5.1	136	6.0	42	1.6
<i>Pongo pygmaeus</i>	2.1	0.21	139	12.5	117	3.9	135	4.7	33	6.7
<i>Hylobates syndactylus</i>	1.8	0.04	154	5.1	118	3.1	144	0.3	34	2.1
<i>Hylobates moloch</i>	1.8		141		116		143		42	
<i>Hylobates pileatus</i>	1.7		154		105		148		32	
<i>Macaca fascicularis</i>	1.5	0.07	149	4.2	116	6.4	144	1.8	38	3.4
<i>Papio ursinus</i>	1.6		141		118		150		44	
<i>Theropithecus gelada</i>	1.6		141		124		146		51	
<i>Mandrillus sphinx</i>	1.8		157		116		146		47	
<i>Colobus guereza</i>	1.7		146		119		150		51	
<i>Presbytis entellus</i>	1.8		137		129		151		56	
<i>Nasalis larvatus</i>	1.9		141		115		147		61	
<i>Cebus apella</i>	1.6		129		125		142		54	
<i>Saimiri sciureus</i>	1.4		133		128		145		42	
<i>Lagothrix lagotricha</i>	1.5		146		125		143		26	
<i>Alouatta seniculus</i>	1.6		138		110		135		30	
<i>Propithecus diadema</i>	1.4		162		95		136		40	
<i>Indri indri</i>	1.4		139		113		134		27	
<i>Microcebus rufus</i>	0.8		127		100		139		45	
<i>Homo sapiens</i> compared with										
<i>Pan troglodytes</i>	***>		**<				***>		***>	
<i>Pan paniscus</i>	***>		**<				***>		***>	
<i>Gorilla gorilla</i>	**>						***>		***>	
<i>Pongo pygmaeus</i>	**>						***>		***>	

¹ Explanation of the measurement codes and symbols in Fig. 1 and Tables 2 and 3. The first angle opens anterolaterally, the other two anterosuperiorly.

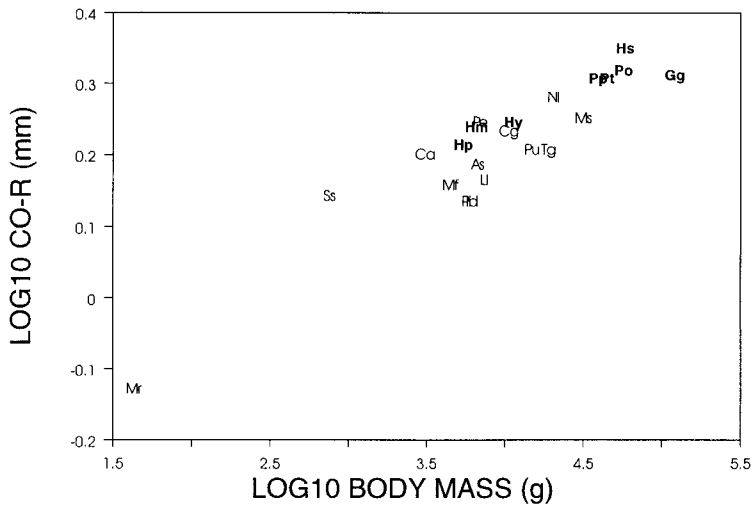


Fig. 9. Bivariate double logarithmic plot between body mass and the radius of curvature of the basal turn of the cochlea (CO-R). Species codes are listed in Table 1, and those of the hominoids are given in bold.

8). When the statistically significant correlation with body mass is taken into account ($r_s = 0.872$; $P < 0.001$), the cochlea of humans is larger than that of *Gorilla*, and *Pan* and *Pongo* are intermediate (Fig. 9). Cochlear size is positively correlated with the size of the posterior and lateral canals

($r_s = 0.580$ and 0.574 , respectively; $P < 0.01$) but not with the anterior canal ($r_s = 0.213$).

The orientation of the basal turn in the transverse plane, relative to either the vertical canals (COt < VSC, Table 8) or the mid-sagittal plane (COt < SG [not listed]), is not significantly different in humans and the

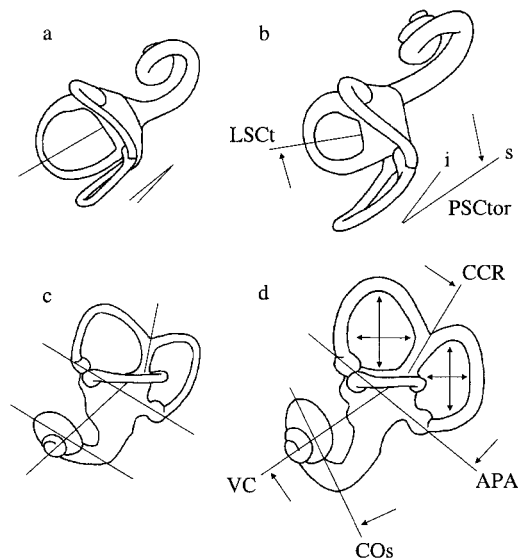


Fig. 10. Superior (a,b) and lateral (c,d) views of the left bony labyrinth of *Pan troglodytes* (a,c) and *Homo sapiens* (b,d) showing major differences between the morphology in humans and great apes. The six differences in orientation of labyrinthine structures are indicated by single-headed arrows, and the large size of the anterior and posterior semicircular canal is indicated by double-headed arrows. Codes as listed in Table 2 and shown in Fig. 1.

great apes, and similar angles are found among many of the other species. However, when seen in lateral view, the human cochlea differs markedly from that of primates other than the colobines. Relative to the level and orientation of the lateral canal, it has a more superior position, its basal turn is more inclined, and its apex faces more anteriorly than inferiorly (Fig. 5). This is shown by the angles of the vestibulo-cochlear axis and of the basal turn, respectively ($VC < LSCm$ and $COs < LSCm$, Table 8).

Correlations

The identification of multiple traits that distinguish the bony labyrinth of humans from that of the great apes raises the questions of whether or not these are correlated, and, if this is the case, whether the human morphology follows the interspecific correlation pattern found among nonhuman primates. The traits concerned are summarized in Figure 10 and Table 9.

Correlations between the radii of curvature of the canals and the cochlea were

TABLE 9. Summary of the angles and index characterizing the human bony labyrinth and basicranium in comparison with the great ape morphology

Bony labyrinth	Basicranium
More coronally oriented Central axis of the lateral semicircular canal (LSCt)	More coronally oriented Posterior petrosal surface (PPp)
Relative to the orientation or level of the lateral semicircular canal (LSCm) Posteriorly tilted common crus ¹ More inclined ampullar line (APA) ¹ More inclined cochlear basal turn (COs) ¹ More superiorly positioned cochlea (VC) ¹ Negative torsion of the posterior semicircular canal (PSCtor) ¹ More inferiorly positioned posterior semicircular canal (SLI), compared with <i>Pan</i> and <i>Pongo</i> only ¹	Relative to the anterior cranial base (s-fc) More inclined basioccipital (ba-s) ¹ More inferiorly facing foramen magnum (o-ba) ¹ More inclined posterior petrosal surface (PPp) ¹

¹ Those features that are correlated in the nonhuman primate sample following a pattern consistent with the human morphology.

discussed above. The height-to-width indices of these structures are not correlated, and neither these indices nor the radii are correlated with the angles or with the sagittal labyrinthine index (r_s values not listed). In particular, Hublin et al. (1996) reported that the radius of curvature of the posterior canal and the latter index are positively correlated among great ape and hominid species, but no such correlation exists for the entire primate sample ($r_s = 0.187$).

Table 10 lists the rank correlation coefficients between the six angles and the sagittal labyrinthine index that characterize the human labyrinth calculated for the nonhuman primate sample. All traits are correlated, with the exception of the axis of symmetry angle of the lateral canal ($LSCt < VSC$) and the torsion of the posterior canal (PSCtor), which are each correlated with two others only. For the two correlations involving $LSCt < VSC$, the human labyrinth does not follow the trend among nonhuman primates (e.g., Fig. 11a), whereas it does for all other correlations (e.g., Fig. 11b). It is worth noting that angles describ-

TABLE 10. Spearman rank correlation coefficients (r_s) between angles and the index of the labyrinth¹

	LSCt < VSC	PSCtor	CCR < LSCm	APA < LSCm	VC < LSCm	COs < LSCm
PSCtor	-0.231					
CCR < LSCm	0.390	-0.547*				
APA < LSCm	0.424	-0.309	0.476*			
VC < LSCm	0.238	-0.114	0.590**	0.627**		
COs < LSCm	0.594**2	-0.501*	0.663**	0.836***	0.548*	
SLI	0.546**2	-0.385	0.723**	0.746***	0.602**	0.838***

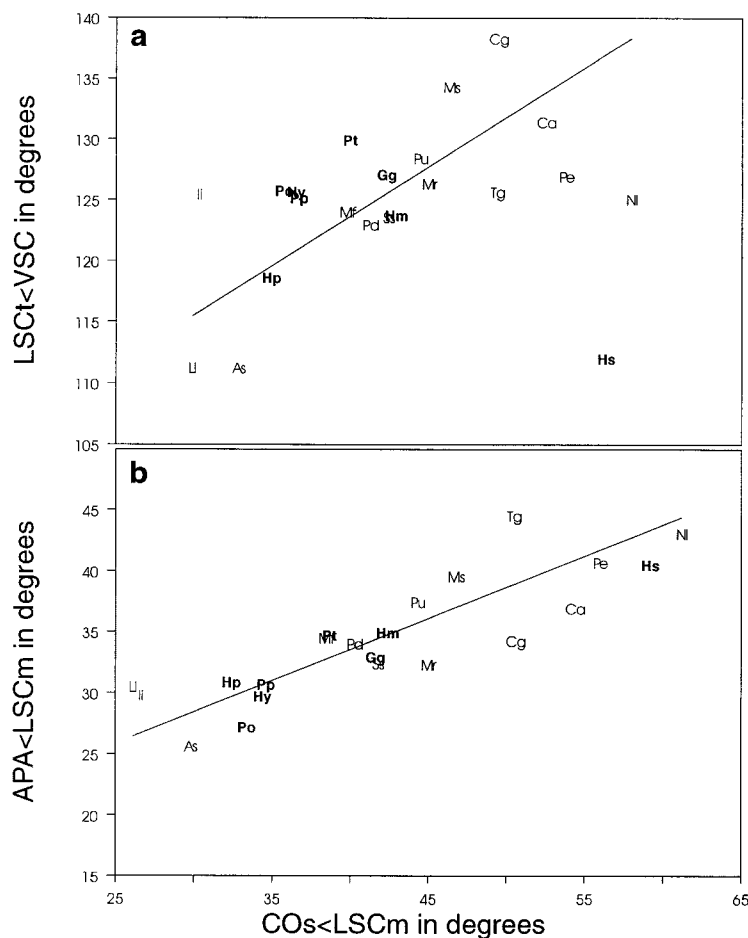
¹ Statistical significance indicated as in Table 3.² Humans do not follow the trend among other primates.

Fig. 11. Bivariate plots between the angles describing the orientations of the cochlear basal turn (COs < LSCm) and (a) the lateral canal axis of symmetry (LSCt < VSC) and (b) the ampullar line (APA < LSCm). Species codes are listed in Table 1; measurement codes are listed in Table 1 and shown in Fig. 1. Correlation coefficients given in Table 10. The reduced major axis regression line for the non-human sample is given.

ing similar parts of the labyrinth, such as the common crus tilt and the posterior canal torsion (CCR < LSCm and PSCtor), are not necessarily more strongly correlated than spatially less related angles, such as the orientations of the ampullar line and the basal turn of the cochlea (APA < LSCm and COs < LSCm).

In conclusion, the human labyrinth consistently differs from that of the great apes with respect to six labyrinthine angles as well as the size of the semicircular canals (Fig. 10; Table 9). To a variable degree, these characters also distinguish humans from primate species other than the great apes (Table 11). Five of the six discriminating

TABLE 11. Presence (y) or absence (n) in primate groups of morphological features characterizing the human bony labyrinth¹

	R of ASC and PSC	R of LSC	LSCt rotated coronally	Sagittal complex rotated
Modern humans	Large	Small	y	y
Great apes	Small	Small	n	n
Hylobatids	Large	Large	n	n
Cercopithecoids	Large	Large	n	y ²
Ceboids	Large	Large/small	n	n
Prosimians	Large	Large	n	n

¹ Measurement codes given in Table 2.

² Except in *Macaca fascicularis*.

angles as well as the sagittal labyrinthine index are correlated among primates in a way that is consistent with the human morphology. The trend common to these correlations is a rotatory deformation in the sagittal plane of the cochlea and parts of the vertical canals around the vestibule and the lateral canal. The rotation is clockwise when viewing the lateral aspect of the left labyrinth (Fig. 10c,d). This morphological complex is not related to the sixth discriminating angle, which concerns the relatively coronal orientation of the human lateral canal axis in the transverse plane (Fig. 10a,b).

Characters that distinguish the human bony labyrinth from other primates show a remarkable similarity to those typifying the human basicranium in general (Table 9). The petrous pyramids are more coronally oriented in humans than in other primates (PPip < SG, Table 12), which corresponds with the more coronally oriented axis of symmetry of the lateral canal. Relative to the anterior cranial base, both the human basioccipital and the posterior petrosal surface have a more inclined orientation, expressing a high degree of basicranial flexion, and the foramen magnum faces more inferiorly (ba-s < s-fc, PPp < s-fc, and o-ba < s-fc, respectively, Table 12). This morphology can be described as a rotation between the posterior and anterior basicranial regions, similar in character to that observed for the labyrinth—that is to say, clockwise when viewing the left lateral aspect of the cranium. In this comparison, the lateral canal orientation appears to be more associated with the anterior basicranium (Table 6) and

the cochlea and aspects of the vertical canals with the posterior basicranium. To investigate whether or not this apparent correspondence between labyrinthine and basicranial traits is unique to humans only, we assessed the interspecific correlation of these traits among the other primates.

The transverse orientations of the posterior petrosal surface and the axis of symmetry of the lateral canal are not correlated among the nonhuman primates, whether the latter is considered relatively to the vertical canals or to the midsagittal plane (PPip < SG and LSCt < VSC or LSCt < SG: $r_s = -0.105$ and -0.102 respectively).

Correlation coefficients calculated for the nonhuman primate sample between angles reflecting the apparent rotation in the sagittal plane of the human labyrinthine and basicranial morphology are listed in Table 13. Furthermore, correlation coefficients were calculated that assess whether or not the orientations of the basioccipital, the posterior petrosal surface, and the foramen magnum covary with those of the cochlea and the vertical canals when both are considered relative to the lateral canal (Table 13). Few labyrinthine angles are directly correlated with basicranial angles, but good correlations were found between parts of the labyrinth and the three aspects of the posterior cranial base.

The torsion of the posterior semicircular canal is correlated only with the foramen magnum orientation (PSCtor and o-ba < s-fc, Table 13). This implies that species with a more posteriorly than inferiorly facing foramen magnum tend to have a human-like negative canal torsion, a trend opposite to the human morphology. The correlation coefficient between the torsion and the sagittal orientation of the posterior petrosal surface is not statistically significant (PSCtor and LSCm < PPp, Table 13). However, a bivariate plot of these angles strongly suggests that, apart from three outliers causing the low coefficient, a correlation does exist (Fig. 12a). Humans, combining a negative canal torsion with a particularly inclined petrosal surface, follow the suggested trend.

None of the correlation coefficients for the common crus orientation are statistically significant (CCR < LSCm, Table 13). In con-

TABLE 12. Basicranial angles describing the orientations of the petrous pyramids, the basioccipital, and the foramen magnum¹

	PPip < SG		PPp < s-fc		ba-s < s-fc		o-ba < s-fc	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Homo sapiens</i>	125	4.4	115	7.5	137	4.9	7	6.4
<i>Pan troglodytes</i>	132	5.2	139	8.0	154	3.6	30	6.0
<i>Pan paniscus</i>	137	7.4	136	8.9	148	9.0	29	8.4
<i>Gorilla gorilla</i>	138	6.7	133	8.3	154	3.6	37	11.1
<i>Pongo pygmaeus</i>	146	4.1	140	3.1	159	6.4	36	8.1
<i>Hylobates syndactylus</i>	148	0.7	155	3.1	173	0.1	46	4.6
<i>Hylobates moloch</i>	144		147		170		46	
<i>Hylobates pileatus</i>	138		162		166		44	
<i>Macaca fascicularis</i>	151	9.4	139	8.8	173	0.6	41	0.0
<i>Papio ursinus</i>	161		143		152		38	
<i>Theropithecus gelada</i>	159		135		156		43	
<i>Mandrillus sphinx</i>	167		132		162		40	
<i>Colobus guereza</i>	161		125		172		56	
<i>Presbytis entellus</i>	153		132		166		50	
<i>Nasalis larvatus</i>	160		134		170		40	
<i>Cebus apella</i>	147		125		167		50	
<i>Saimiri sciureus</i>	167		153		169		45	
<i>Lagothrix lagothricha</i>	163		147		175		45	
<i>Alouatta seniculus</i>	169		144		185		70	
<i>Propithecus diadema</i>	181		149		185		73	
<i>Indri indri</i>	172		144		173		57	
<i>Microcebus rufus</i>	160		148		178		56	
<i>Homo sapiens</i> compared with								
<i>Pan troglodytes</i>	**<		***<		***<		***<	
<i>Pan paniscus</i>	***<		***<		***<		***<	
<i>Gorilla gorilla</i>	***<		***<		***<		***<	
<i>Pongo pygmaeus</i>	***<		***<		***<		***<	

¹ Explanation of the measurement codes and symbols in Fig. 1 and Tables 2 and 3. The first angle opens anterolaterally, the others anteroinferiorly.

TABLE 13. Spearman rank correlation coefficients (r_s) between angles and the index of the labyrinth and the basicranium¹

	PSCtor	CCR < LSCm	APA < LSCm	VC < LSCm	COs < LSCm	SLI
ba-s < s-fc	-0.363	-0.134	-0.332	-0.253	-0.248	-0.336
o-ba < s-fc	-0.550* ²	0.104	-0.181	-0.131	0.006	-0.184
PPp < s-fc	0.166	-0.213	-0.546*	-0.217	-0.614**	-0.513*
LSCm < ba-s	0.029	0.376	0.658**	0.494*	0.559*	0.579**
LSCm < o-ba	0.089	0.282	0.673**	0.545*	0.437	0.515*
LSCm < PPp	-0.358	0.411	0.841***	0.443*	0.840***	0.645**

¹ Statistical significance indicated as in Table 3.

² Humans do not follow the trend among other primates.

trast, the orientations of the ampullar line (APA < LSCm), the cochlear basal turn (COs < LSCm), and the sagittal labyrinthine index (SLI) all show correlations with those of the basioccipital, the foramen magnum, and particularly the posterior petrosal surface (e.g., LSCm < PPp to COs < LSCm, Fig. 12b). In each case, the human morphology is in accordance with the interspecific trend. The orientation of the vestibulo-cochlear line (VC < LSCm) shows similar correlations, although mostly with lower coefficients. Interestingly, a bivariate plot between the vestibulo-cochlear line and the

foramen magnum angle to the anterior cranial base (o-ba < s-fc) reveals two parallel regressions, one for the great apes and humans ($r_s = -0.800$, not significant), and one for other primates ($r_s = -0.593$, $P < 0.05$) (Fig. 13).

In summary, the complex of labyrinthine traits and the aspects of the posterior basicranium, both of which show a rotated morphology in the sagittal plane in humans, are correlated among primate species. The human morphology is consistent with the trends of these interspecific correlations. In contrast, the posterior petrosal surface and

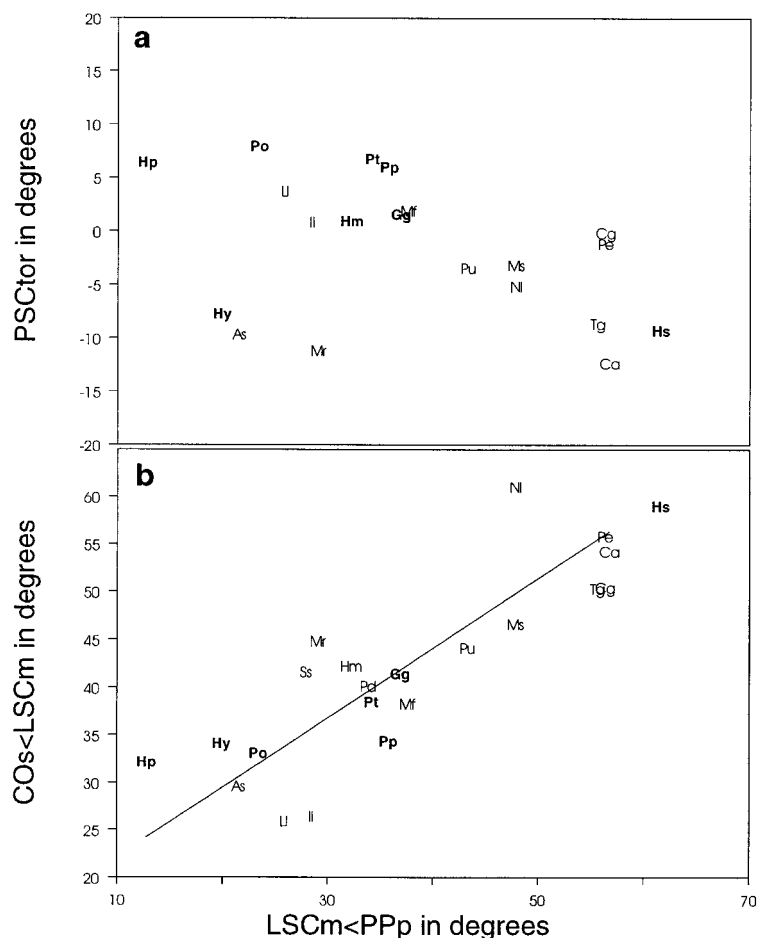


Fig. 12. Bivariate plots describing the relationship between the orientations of the posterior petrosal surface (LSCm < PPp) and (a) torsion of the posterior canal (PSCtor) and (b) the cochlear basal turn (COs < LSCm). Species codes are listed in Table 1; measurements codes are listed in Table 1 and shown in Fig. 1. Correlation coefficients given in Table 13. In panel b, the reduced major axis regression line for the nonhuman sample is given.

the lateral canal axis, both of which in humans have a markedly coronal orientation, are not interspecifically correlated.

PHYLOGENY

The morphometric comparisons presented in this study reveal considerable differences between the bony labyrinths of humans, the great apes, and other primate species, both with respect to the size of the semicircular canals and the spatial orientation between labyrinthine structures (Table 11). All four great ape species share the same morphological pattern, and it seems therefore likely that this also represents the character state of their common ancestor as well as that of humans and the African apes. This hypothesis is supported by preliminary investigations of fossil specimens, which indicate that

the morphology seen in the extant great apes is also found in the hominoid *Dryopithecus branchoi* from 10 million-year-old deposits at Rudabanya (Spoor, 1996) as well as in South African australopithecines (Spoor and Zonneveld, 1994b; Spoor et al., 1994). This implies that the differences between the human and great ape labyrinths must have emerged in the course of human evolution. It also follows from this conclusion that the closer similarity of the human labyrinthine morphology to that of (large) cercopithecoids than to that of the great apes, as indicated by Table 11, is the result of homoplasy. The ancestral labyrinthine morphology of the anthropoids, and perhaps all primates, is most likely close to that shared in the sample by hylobatids, *Macaca*, ceboids, and prosimians. Apart from this general pattern,

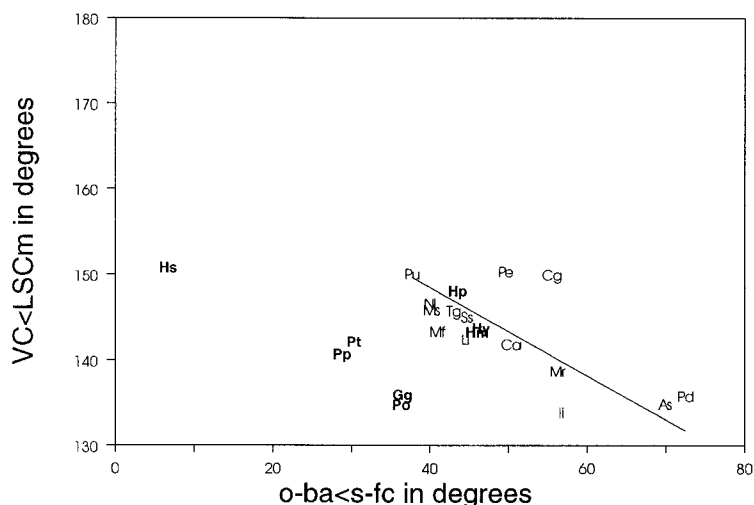


Fig. 13. Bivariate plot between the basicranial angle describing the foramen magnum orientation ($o-ba < s-fc$) and the labyrinthine angle of the vestibulo-cochlear line ($VC < LSCm$). Species codes are listed in Table 1; measurements codes are listed in Table 1 and shown in Fig. 1. Correlation coefficients are given in Table 13 and the text. The reduced major axis regression line is given for the sample excluding the large-bodied hominoids.

individual taxa show specific traits, such as the shape of the lateral canal and the common crus in *Pongo*. However, for species other than the great apes and humans, larger samples would have to be investigated for these to be identified with any confidence.

The key issues that are central to evaluating the labyrinthine diversity found among primates are the link of semicircular canal morphology to vestibular function and locomotor behavior as well as mechanisms underlying the correlations between labyrinthine shape and basicranial architecture. Insight into these biological factors is required as a framework for the interpretation of fossil specimens and is a prerequisite for the use of labyrinthine traits in phylogenetic analyses.

FUNCTIONAL MORPHOLOGY

The dimensions and shape of the bony labyrinth reflect, to a variable degree, those of enclosed membranous structures that are part of the sense organs of the auditory and vestibular systems. It is worth briefly considering any functional aspects of the other parts of the bony labyrinth before focussing on the semicircular canal system. Cochlear size relates to basilar membrane length, but, unlike width and thickness, this property yields little information on hearing capacity (Ketten, 1992; Echteler et al., 1994). This, and the fact that the measurements in

this study are restricted to the basal turn only, means that no functional conclusions can be drawn from the observation that the cochlea is larger in humans than in great apes, *Gorilla* in particular. However, no major differences related to cochlear function can be expected because auditory characteristics of humans and chimpanzees are close and do not vary widely among anthropoids in general (Newman, 1988; Stebbins and Moody, 1994).

The vestibule of the bony labyrinth contains the utricular and saccular otolith organs, which comprise the component of the vestibular apparatus registering linear head acceleration and gravity. The bony vestibular morphology is unlikely to reflect any functional aspects, in particular when assessed with the limited resolution of CT scans, because of the loose spatial relationship with the membranous parts. Histological serial sections of the vestibular region of the chimpanzee, the orangutan and humans reveal no differences related to function of the otolith organs (Altmann and Vermes, 1933).

The semicircular canal system, the other component of the vestibular apparatus, records angular head movements, and here bony morphology is associated with function in the form of the arc sizes and planar orientation of the canals. The best understood role of the system is its sensory input into the highly effective reflex stabilization

of gaze during body movements (see reviews in, for example, Wilson and Melvill Jones, 1979; Leigh and Brandt, 1993; Schwartz and Tomlinson, 1994). Stabilization is achieved by compensating body and head movements through the vestibulocollic reflex working on the neck musculature and, more importantly, the vestibulo-ocular reflex working on the extraocular muscles. The ability to avoid blurred vision during locomotion is vital to animals such as primates, which heavily rely on visual clues when navigating the environment. Angular head stabilization also provides a simplified vestibular signal, which helps in the measurement of linear motion by the otolith organs during complex movements (Wilson and Melvill Jones, 1979; Pozzo et al., 1990, 1992).

Through the vestibulospinal reflexes, the semicircular canal system also contributes to the coordination of body movements during locomotion of both quadrupedal mammals and humans (Money and Scott, 1962; Suzuki and Cohen, 1964; Schor and Miller, 1981; Solomon and Cohen, 1992; Igarashi et al., 1988; Ito and Hinoki, 1991; Ito et al., 1992). The role of the semicircular system in maintaining posture is more controversial (for a review see Dietz, 1992). Nevertheless, studies of human postural control have demonstrated the importance of vestibular information (Trippel et al., 1992; Petersen et al., 1994), with the semicircular canals responding to body sway frequencies over 0.1 Hz (Nasher et al., 1989; Kleiber et al., 1990). Balance corrections appear to be modulated by vestibular input, whereas they are triggered by proprioceptive signals only (Kleiber et al., 1990; Allum et al., 1995). In general, contributions of the semicircular canal system to the sensory control of posture and locomotion should not be seen in an isolated context but as part of the highly integrated vestibular, visual, and proprioceptive input.

Arc size of the semicircular canals

Investigating the functional significance of the arc size of the semicircular canals in relation to locomotor behavior is complex because limited evidence from different disciplines needs to be integrated (Fig. 14). In a comparative anatomical approach, the ques-

tion can be asked whether among a wide range of species a purely empirical correlation can be found between types of locomotor behavior and aspects of semicircular canal morphology, the arc size in particular. Important in this context are the general scaling relationship between canal dimensions and body size between large groups of vertebrates, specific trends between more closely related taxa, and the residuals of individual species from any such trend. The latter represent biological specialization and the key to understanding possible links between canal size and behavior.

Following the question of if and how canal size correlates with body mass and locomotor behavior, the why can be explored by assessing the biophysical ground for any such relationship. Hydrodynamical models of the vestibular apparatus can be used to predict how duct and canal dimensions relate to functionally important characteristics of the canal system, such as sensitivity and response time. It is these characteristics that must match the frequency range of angular head movements typical for a species' locomotor behavior. Hence, it is important that representative frequency spectra of head movements are known to confidently associate canal morphology with types of locomotion. However, at present such kinematic analyses are not available for primates other than humans (Grossman et al., 1988; Keshner and Peterson, 1992; King et al., 1992). Nevertheless, some basic requirements of the canal system can be inferred by considering strongly simplified and contrasting categories of locomotor behavior, such as agile and acrobatic vs. slow-moving and cautious.

Before specifically considering the functional significance of the canal arc sizes in humans and the great apes, we will review in somewhat more detail the broad comparative and biophysical evidence schematized in Figure 14.

Comparative evidence. The general scaling relationship between semicircular canal dimensions and body size has been investigated interspecifically among groups of vertebrates and intraspecifically during growth of fish species (Jones and Spells, 1963; Ten

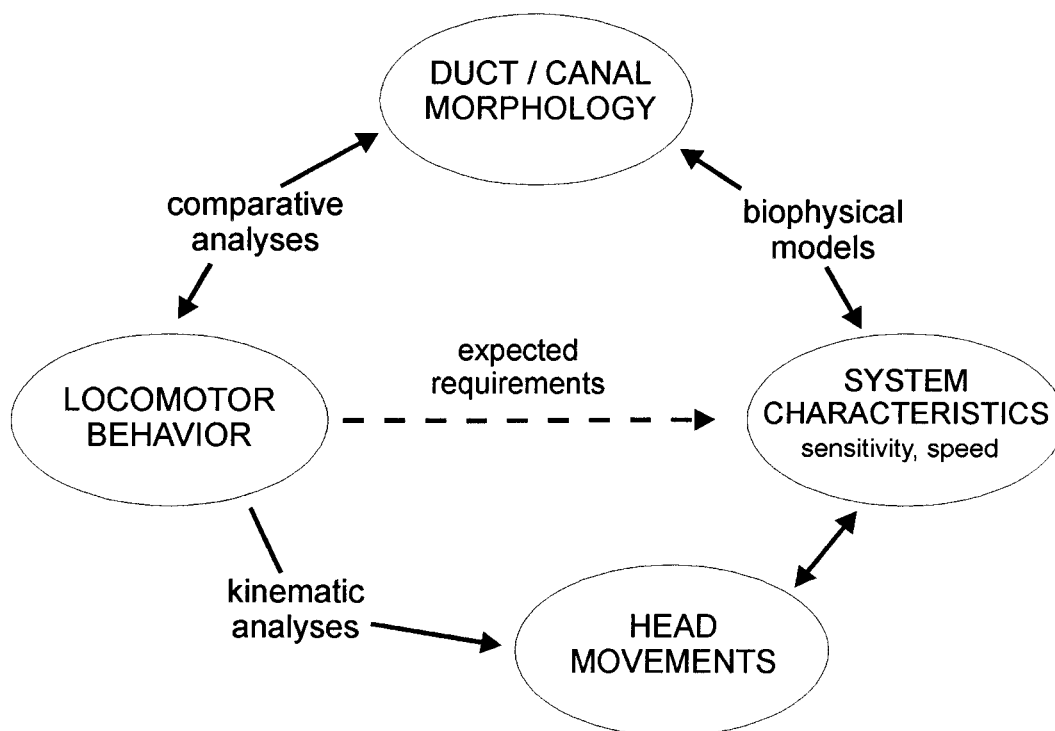


Fig. 14. Flow chart summarizing possible approaches of assessing the relationship between the morphology of the semicircular canal system and locomotor behaviour.

Kate et al., 1970; Howland and Masci, 1973; Muller, 1990). The present analysis of scaling among nonprimate mammals (Fig. 7) is based on the same sample as used in previous studies, Jones and Spells (1963) in particular, and the results can thus not be verified independently. Plotting duct radii of curvature against body mass, Jones and Spells (1963) found a regression slope of 0.08 for their total sample of mammals, birds, reptiles, and fishes, a value not strikingly different from the slopes of 0.14 obtained in the present study for the canal radii of both primates and other mammals² (Fig. 7). Thus, it appears that throughout different vertebrate groups the semicircular ducts and canals tend to show a basic scaling factor, which results in a small, negative-allometric increase with body mass, separate from

more taxa-specific differences. To put the scaling factor into perspective, the canal radius of curvature increases about fivefold from the house mouse to the Asiatic elephant (Fig. 7).

A number of comparative studies of the bony labyrinth have previously associated semicircular canal size and locomotor behavior, with the common observation that more agile species have larger-arc'd canals than slow-moving ones. In birds, the semicircular canals have been described as large in species showing a high degree of maneuverability, such as pigeons and raptors, and small in species characterized by stability of flight, including ducks and geese (Tanturri, 1933; Turkewitsch, 1934; Hadziselimovic and Savkovic, 1964). Owls, which have little eye movement and mainly achieve retinal stabilization through head movements, have particularly well-developed canals (Tanturri 1933; Hadziselimovic and Savkovic, 1964; Money and Correia, 1972).

²Detailed comparison between Jones and Spells (1963) and the present study is not possible because the former used estimated radii of curvature of whatever duct is visible in the photographs of labyrinths in Gray (1907, 1908) instead of radii of all three canals, calculated from Gray's actual measurements (see also Spoor et al., 1996).

In his survey of the mammalian labyrinth, Gray (1907, 1908) drew attention to the small canals of the three-toed sloth *Bradypus tridactylus* and associated this morphology with its sluggish behavior. He also described the greatly reduced canal sizes in the right whale *Eubalaena glacialis* and the common porpoise *Phocaena phocaena*, an observation corroborated here in Figure 7.

Dramatic reduction of the semicircular canals in cetaceans was initially observed by Hyrtl (1845) and more recently described by Ketten (1992). This phenomenon, unknown in nonaquatic taxa, has been associated with limited neck motility, marked by fusion of the cervical vertebrae (Gray, 1908; Ketten, 1992). Cetaceans, whale species in particular, also show reduced eye motility, marked by underdevelopment of most extraocular muscles (Hosokawa, 1951; Prince, 1956; Pilleri and Wandeler, 1964). Thus, it is likely the concurring absence of strong vestibulocollic and vestibulo-ocular reflexes that results in degeneration of the canal system.

That visual regression on its own does not necessarily lead to a degenerated semicircular canal system is shown by two unrelated species of subterranean mole rats (*Cryptomys* and *Spalax*). Relative to body mass, these species were found to have larger ducts than the brown rat, and a specialized role other than gaze stabilization, possibly in navigating the complex maze of their burrow system, has been proposed (Lindenlaub et al., 1995). It is not clear, however, if these differences in canal size relate to specific frequency patterns of head movements.

In the only previous study specifically examining primate semicircular canal dimensions in relation to locomotor behavior, Matano et al. (1985, 1986) found that, taking body mass into account, the rapid leaper *Tarsius bancanus* has significantly larger canals than both the slow-climbing *Nycticebus coucang* and other mammals listed by Jones and Spells (1963). The present study confirms their conclusion and indicates that the distinction is most striking for the lateral canal (Figs. 6c, 8c). *Tarsius* is similar to owls in that its eyes are almost immobile in the orbits and that retinal stabilization is entirely achieved through head rotations

(Castenholz, 1984). In both, the resulting pattern of fast, active head movements corresponds with markedly large canals. That it is the lateral canal that is particularly large in *Tarsius* can perhaps be associated with its unique ability to rapidly rotate its neck over 180° to either side (Schultz, 1969; Castenholz, 1984; Nowak, 1991).

Other results of the current study further support a link between relatively large canal size and agility. Among the hominoids, the semicircular canals of the brachiating hylobatids are consistently larger than those of the less agile great apes using forms of arboreal or terrestrial quadrupedalism. Likewise, among the atelines the canals of *Ateles*, employing a rapid suspensory mode of locomotion, are larger than those of the slow, quadrupedal *Alouatta* (for a comparison of ateline locomotor behaviors see Strier, 1992). The more general observation that primates as a group tend to show relative large semicircular canals among mammals (Fig. 7) fits the notion of these species as particularly agile and visually oriented.

Biophysical models. Explanations of why the arc dimensions of the semicircular canals increase with body size and appear to be related with aspects of locomotor behavior must be sought in the biophysics and physiology of the canal system. The traditional model of the semicircular canal system, proposed by Steinhausen (1933) and further developed by Van Egmond et al. (1949), assumes that the system behaves as a heavily dampened torsion pendulum and considers the cupula as a watertight swinging door. In this model, the endolymph and cupular motion are characterized by a short and a long time constant, which describe the response time to attain maximum displacement and the restoration or recovery time to passively return to the initial state, respectively. As far as the influence of the duct dimensions is concerned, the short time constant increases with the lumen size and the long time constant with both the lumen size and the radius of curvature of the arc. Among mammals, typical estimates of the short time constant are in the order of milliseconds and those of the long time constant in the order of seconds (Curthoys et

al., 1977b; Fernandez and Goldberg, 1971; Oman and Young, 1972; Oman et al., 1987; Ramprashad et al., 1984; Wilson and Melvill Jones, 1979). Subsequent studies either extended this model or invoked alternative concepts, but in each of these the system's sensitivity is proportional to the radius of curvature of the duct (Ten Kate et al., 1970; Oman et al., 1987; Muller and Verhagen, 1988a,b).

Jones and Spells (1963) were the first to assess the biology behind the general scaling effect shown by semicircular duct dimensions. After all, for a sensor system where size affects function, it is not immediately obvious why, as a general trend, the sensor dimensions slightly increase with body size. The hypothesis proposed by Jones and Spells (1963) is that larger animals tend to make more sluggish head movements and require a more sensitive canal system to maintain similarity of response. Using the torsion pendulum canal model, they proposed that this is achieved by increasing both the lumen size and the radius of curvature of the ducts. Modelling the allometry of head movements, they derived theoretical relationships between body mass and the two dimensions, which approximately correspond with correlations empirically determined from labyrinths shown in Gray (1907, 1908).

Melvill Jones (1974) and Wilson and Melvill Jones (1979) further discussed the mechanism underlying the relations found by Jones and Spells (1963). Examining the frequency response of the torsion pendulum model, they pointed out that over a limited range the canal system works as an angular velocity transducer and proposed that the limits of this range are adjusted according to the frequency content of normal head movements. Thus, to maintain accurate angular velocity transduction, "small animals with short-sharp head movements would require these limits to move up the frequency scale; in large animals with more ponderous head movements the limits should move down the scale" (Wilson and Melvill Jones, 1979:55). The proposed mechanism by which this is achieved is the decrease and increase, respectively, of the lumen size and the radius of curvature of the semicircular duct, because the cutoff frequencies of the range depend on

these dimensions (the cutoff frequencies being the inverse of the short and long time constants).

If the semicircular canal system attunes to the changing frequency spectrum of head movements associated with differences in body size, as proposed by Jones and Spells (1963) and Wilson and Melvill Jones (1979), it is no less logical that this match through the duct dimensions will also apply to similarly sized animals showing markedly dissimilar, locomotor-related head movements. Indeed, both studies extend their hypothesis beyond a general scaling effect when stating that canal sensitivity "requires adjustment in order to match the likely pattern of head movements . . . according to size shape and habitat of the animal" (Jones and Spells, 1963:416) and that "the data generally support the theory that the dimensions of the semicircular canals attune them to the angular frequency spectra of the animal's natural movement in its natural habitat" (Wilson and Melvill Jones, 1979:58).

When considering the properties of the semicircular system in the context of actual animal behavior, Muller (1990, 1994) pointed out that the system is more likely to be adapted to irregular, step-like movements than to the regular sinusoidal movements of laboratory experiments. He questioned the biological importance of the requirement of pure angular velocity transduction, and, given that animals rarely make continuous head movements lasting several seconds, that of the long time constant. Instead, Muller stressed the importance of the short time constant, indicating the response speed and the normalized maximum endolymph displacement as a measure for the sensitivity of the system. These two properties indeed seem pivotal when considering the requirements for primate species with widely contrasting locomotor behaviors and when bringing together the evidence from the models and the empirical observations.

Combining the evidence. Locomotion of rapid leapers and brachiators is characterized by strong acceleration and deceleration and frequent change of direction. Hence, the system cannot be too sensitive, as this would lead to overstimulation, but response times

must be short to keep track of the changing movements. In contrast, slow quadrupedal climbers are expected to require a higher sensitivity, but response times are less crucial. Given that the increase of a duct's lumen size results in longer response times and the increase of the radius of curvature in higher sensitivity, the ducts of slow-moving species are expected to have a large radius with a wide lumen and those of agile species a smaller radius with a more narrow lumen. This is consistent with the hypothesis of Jones and Spells (1963), which links larger, more sluggish species with larger duct dimensions. However, these predictions are inconsistent with the comparative evidence, which indicates that it is the more agile species that tend to have larger-arc ducts and canals. This striking contradiction between the models and the comparative evidence has been noted previously by Curthoys et al. (1977a).

If the comparative evidence correctly correlates large canals with fast head movements, this should not apply only to diverse locomotor behaviors but also to the general scaling effect shown by the canals. Although an increase of sluggishness with body size appears intuitively correct, it would be worth exploring the speculative alternative that, all other things being equal, labyrinths tend to experience greater and not smaller velocities and changes of velocity in larger species because they are further removed from centers of head and body rotation. The main issue where the theoretical and comparative evidence appears to be difficult to reconcile is the implication of the models that the larger canals of agile species are more sensitive to angular motion than those of slow-moving species.

Given the discrepancies between the theoretical and comparative evidence, it is worth briefly considering the limitations of either approach. The biophysical models are characterized by unavoidable simplifications of the vestibular system, and there is uncertainty over important aspects such as the nature of cupular movement (e.g., see the discussion in Muller, 1994). Virtually all models pertain to a single canal, and even in this simplified context increasingly sophisticated descriptions of the fluid mechanics

predict frequency responses different from the torsion pendulum model (Oman et al., 1987; Rabbitt and Damiano, 1992). The one published model based on all three canals gives a hint of the complexity of the actual biological reality (Muller and Verhagen, 1988a,b). Owing to hydrodynamical interaction between the parts of the vestibular system, change of any of the duct dimensions or of the angles between the duct planes simultaneously influences the time constants and sensitivity of all ducts.

Another complication with the theoretical approach is that it is not entirely clear what properties of the model are truly important for the canal system to function in a biological setting. Whereas Muller (1990, 1994) justifiably argued that the long time constant has little biological value, Oman et al. (1987) indicated that the values of the short time constant (i.e., the response speed), estimated for a few species, are too small to have physiological significance. Despite being defined in different ways (Ten Kate et al., 1970; Oman et al., 1987; Muller, 1994), canal sensitivity appears thus far to be the undisputed property of biological significance. Some support for a positive correlation between canal size and sensitivity, as predicted by the models, comes from experimental evidence. Studies based on measurements of peripheral afferent nerve responses in the cat and the squirrel monkey, which suggests that within a labyrinth the largest canal is the most sensitive one (Goldberg and Fernandez, 1971; Blanks et al., 1975; Curthoys et al., 1977a).

The major limitation of the comparative morphological evidence considered here is that it concerns only the radius of curvature of each bony canal as an approximation of the arc size of the membranous duct, whereas the sensitivity and response time also depend on properties such as the duct's lumen size and the dimensions of the ampulla and the utricle. Some aspects are, however, less important in a comparative context. The viscosity and density of the endolymph are considered to be more or less constant among mammalian species (e.g., Curthoys et al., 1977b; Ramprasad et al., 1984). Moreover, the elastic properties of the cupula influence only the biologically less relevant long time

constant of the system (Muller, 1990). Collecting more complete comparative morphometric datasets of the fragile membranous labyrinth requires fixation of the inner ear immediately after death followed by either dissection or serial sectioning (Curthoys and Oman, 1986, 1987; Lindenlaub et al., 1995). In practice, this is difficult in the case of primate species other than those used in laboratory experiments.

Finally, an important limitation common to both the comparative and theoretical approach is the lack of data describing actual frequency spectra of head movements in different species. Such kinematic analyses are crucial to underpin qualitative terms such as *agile*, *slow-moving*, or *sluggishness* and its presumed increase with body size and to test the biological relevance of system characteristics such as the response speed.

In sum, the hypothesis that semicircular canal dimensions are at least to some extent correlated with natural head movements and thus locomotor behavior is supported by the basic physics of the system design as well as by comparative morphological studies. That current theoretical and comparative evidence on the exact nature of this link appears to be contradictory does not necessarily disprove the link itself. Rather, it demonstrates that comparative aspects of functional vestibular morphology are still poorly understood because of the biophysical complexity of the semicircular canal system and the lack of morphometric and behavioral data. When all available evidence is weighed, it seems that the very basic, empirically determined link associating relatively large-arc semicircular canals with agility and rapid movements currently offers the biologically most useful working hypothesis.

Great apes and humans. The notion that semicircular canal size has functional significance raises the question of what possible factors underlie the larger vertical canals of humans when compared with the great apes. However, this issue cannot be seen separately from a second question asking why the great apes, representative of humans' ancestral condition, tend to have smaller canals than expected on the basis of the general trend among other primates.

Following the comparative evidence, smaller canals suggest head movements that are on the whole slower than what would be expected for a hypothetical monkey of great ape size. Whereas it is easy to appreciate that great apes and hylobatids show contrasting frequency patterns of head movements, it is more difficult to identify specific elements of great ape behavior that are evidently linked with an overall frequency shift of head movements relative to large cercopithecids.

The great ape anatomy most likely linked with distinct head and body movements is their short hind limbs relative to body mass, the particularly robust shoulder region, and the bulky proportions of the neck when compared with nonhominoid primates and humans (Schultz, 1933, 1969; Aiello and Dean, 1990). Although this body build intuitively suggests the slower head movements predicted by the comparative canal data, this is by no means certain. For example, viscoelastic properties of the neck play a role in stabilizing the head during locomotion (Guitton et al., 1986; Keshner and Peterson, 1992), and more bulky neck proportions could therefore result in diminished passive stabilization and an actual increase of head movements. The hylobatids share many aspects of the great ape body build associated with above-the-head use of the arms, but it is the rapid whole body movements associated with brachiation as opposed to quadrumanous climbing and terrestrial locomotion that is the most likely dominant factor underlying their larger semicircular canal sizes.

The most obvious factor to be considered in relation to human semicircular canal size is upright bipedal locomotion and the associated pattern of head movements. What is particularly striking in humans is that only the arcs of the vertical canals and ducts are enlarged and not that of the lateral duct. The lumen sizes, in contrast, are virtually identical for all three ducts (Curthoys et al., 1977b).

Given the comparative evidence, the vertical canals of humans could be expected to be associated with somewhat more rapid head movements than the lateral one. Indeed, Grossman et al. (1988) and King et al. (1992) found that human head rotations, measured

during walking and running, showed predominant frequencies between 2 and 8 Hz in sagittal and coronal planes (pitch and roll) that were significantly higher than those between 1 and 3 Hz in the horizontal plane (yaw). There is also evidence from threshold determinations and subjective response studies that the lateral canal is somewhat more sensitive than the vertical canals (Guedry, 1974; Benson and Brown, 1992). Hence, in both cases this experimental evidence is consistent with the predictions from the comparative data and not with the theoretical models which would predict that the vertical canals are the more sensitive ones. King et al. (1992) associated the human frequency pattern of head movements with upright bipedal locomotion in which two steps correspond with one complete horizontal head rotation, whereas the head moves up and down synchronously with each step. The spectrum of great ape head movements will likely differ significantly, given that quadrupedal locomotion is characterized by a more complex cycle of limb movements and that the head is not consistently positioned over the moving limbs. However, establishing the nature of such differences and whether they can be correlated in any way with the observed canal dimensions will be dependent on future analyses of head rotation frequencies in nonhuman primates.

Apart from dealing with different patterns of head movements in the context of head and gaze stabilization, it is possible that in humans the semicircular system plays an extended role in regulatory processes typical for bipedal locomotion. Ito and Hinoki (1991) investigated semicircular canal function during circular walking of humans and quadrupeds. In the latter, the medial vestibulospinal tract, supplied from the semicircular canals, descends only to the upper thoracic levels of the spinal cord. In humans, however, they reported evidence to support the concept that impulses from the semicircular canals reach the lumbosacral cord and influence lower as well as upper extremity activity. In particular, the vestibulospinal reflex has the effect that during human circular walking the lateral canal output causes increased antigravity muscle tonus of the inner leg, thus giving assistance

in support of the shifting body weight (Ito et al., 1992).

What makes humans especially interesting in the study of the relationship among semicircular canal size, vestibular function, and locomotor behavior is not just the concurrence of enlarged vertical canals and unique primate behavior in the form of habitual bipedalism but also the existence of a well-studied fossil record of human evolutionary history. Thus, detailed analysis of hominid remains makes it possible to pinpoint in what taxa and what period canal enlargement occurred and to compare such findings with postcranial evidence on the emergence of habitual bipedalism. Sporer et al. (1994), in a preliminary study of fossil hominid labyrinths, have demonstrated that *Homo erectus* shows modern human canal dimensions. In contrast, South African australopithecines show the ancestral great ape-like condition, which has been interpreted as support for studies concluding that these hominids were facultative rather than obligatory bipeds. Subsequently it was discovered that Neanderthals, as habitual bipeds, nevertheless have smaller vertical canals than modern humans (Hublin et al., 1996). If *H. erectus* is ancestral to all later forms of the genus *Homo*, this would imply that the Neanderthal canal dimensions represent a derived rather than ancestral condition. Hence, the evolutionary history of the hominid semicircular canal system is clearly more complex than a single change from a more great ape-like to a modern human-like morphology, and any link with locomotion exceeds a simple association with the broad categories of quadrupedal vs. bipedal behavior. An aspect of the Neanderthal morphology that deserves further investigation, because of its potential relation with frequency patterns of head movement, is Neanderthal neck proportions. Whereas modern humans clearly have a more slender neck than the great apes (Schultz, 1933, 1969), this may be less pronounced in Neanderthals. For example, the cervical segment forms a relatively short 16% of the total spine length of the Kebara 2 skeleton, whereas a mean value of 22% was obtained for modern humans (Arensburg, 1991).

Finally, a last aspect of semicircular canal size to be considered is the possible significance of the wider perilymphatic space surrounding the semicircular ducts in humans than in other primates (Hyrtl, 1845; Gray, 1907; Ramprashad et al., 1984). Although some studies have proposed that the perilymph plays a significant role in semicircular canal mechanics (Rejtoe, 1939; Anliker and Van Buskirk, 1971), others have convincingly demonstrated that this is very unlikely, mainly because the dense trabecular pattern in the perilymphatic space prohibits free fluid movement (Dohlman and Kühn, 1973; McCabe and Ryu, 1973). It seems most likely that the diversity in primates of the ratio between the lumen sizes of the membranous ducts and the bony canals reflect interspecific differences of otic capsule development affecting the bony lumen.

Semicircular canal orientation

Planar orientations of the semicircular canals of primate species have been reported in comparative studies (Denker, 1899a,b; Berg, 1903; Perez, 1922; Girard, 1923; Delattre and Fenart, 1960; Cousin et al., 1981; Matano et al., 1985, 1986) as well as in analyses aimed at integrating anatomical and physiological aspects of the canal system (Blanks et al., 1985; Reisine et al., 1988). The angles of the anterior semicircular canal relative to the midsagittal plane reported in the current study ($ASCm < SG$, Table 6) tend to be in correspondence with mean values reported previously for humans (36–41° in Blanks et al. [1975], Colosi and Giannardi [1971], and Caix and Outrequin [1979]) and other primates (34–44° in Blanks et al. [1985] and Matano et al. [1985, 1986]). On the other hand, the values given in these studies for the posterior canal (121–128° for humans, 123–130° for other primates) are consistently smaller than those obtained here ($PSCm < SG$, Table 6). The reason for this is that these earlier studies excluded the common crus from the arcs of the posterior and anterior canals. Owing to the nature of the canal torsions, this has little effect on measurements of the anterior canal orientation but leads to angles indicating a more coronal orientation of the posterior canal than indicated by the present

study, which does include the common crus. The current results may well prove biologically more useful, because Reisine et al. (1988) found that including the common crus in the anatomical planes results in closer correspondence to the experimentally identified physiological planes of maximum sensitivity. Ideally the CT measurements could nevertheless be improved in future analyses by taking landmarks along the entire arc of the canal rather than at the greatest width of the arc only. Regardless of the method of measuring, past and present evidence supports the notion that vertical canal orientations are similar among a wide range of primates, without specific differences between humans and most other species.

Of the angles used here to describe the planar orientation of the lateral semicircular canal in the cranium, only the angle relative to the foramen magnum is given in previous comparative studies (Perez, 1922; Girard, 1923; Delattre and Fenart, 1960; Caix and Outrequin, 1979; Cousin et al., 1981). The mean values reported in these studies, 9–16° for humans and 33–80° for other primates, are close to those in Table 6 ($LSC < o-ba$). In addition, Cousin et al. (1981) measured angles between the lateral canal and the midsagittal orientations of the surface of the clivus and the line sella to nasion for humans (52 specimens), *Pan troglodytes* (42 specimens), and *Pan paniscus* (59 specimens). To enable comparison, we measured these same angles for the samples of the present study, and the differences between the means of not more than 4° are not statistically significant.

The observation that the angle of the lateral canal to the external basicranial orientation is similar in humans and the African apes ($LSCm < ba-na$, Table 6) cannot be compared with previous findings, as this angle has not been measured before. However, overall stability is supported by the finding of Cousin et al. (1981) that the angle between the lateral canal and the Frankfurt Horizontal plane is very similar indeed in humans, *P. troglodytes*, and *P. paniscus* (22°, 21°, and 23°, respectively). A clear but indirect indication of planar stability of the lateral canal in the cranium is also

given by the fact that in the present study CT scans made in the nasion-biporionic plane consistently show the full extent of the lateral canal in all species except *Indri indri*. However, it should be remembered that the 1.5 mm slice thickness can allow for a degree of deviation from the scan plane depending on the arc and lumen size of the canal.

Given the diversity of basicranial architecture and labyrinthine morphology among primate species, it is remarkable that planar stability of the semicircular canals is maintained, especially when it can be argued that, as long as the three canals of each labyrinth have an approximately perpendicular orientation among each other, all possible angular head movements can be perceived, no matter the overall orientation in the cranium. An extensive number of studies have promoted head posture as the dominant factor underlying planar stability of the lateral canals, based on the hypothesis that animals hold their head so that these canals are aligned with earth horizontal (Perez, 1922; Girard, 1923; Lebedkin, 1924; for a brief review of later studies see Fenart and Pellerin [1988]). However, this is not supported by studies recording head posture of humans and animals, which consistently found that the lateral canal has an inclined orientation relative to earth horizontal (De Beer, 1947; Mazza and Winterson, 1984; Erichsen et al., 1989; Graf et al., 1995).

Rather than the static head posture of animals in a state of rest or vigilance being a focus, it would be worth investigating whether the orientation of the lateral canals corresponds with the predominant plane of natural yaw movements of the head during locomotion. Another possible factor constraining the lateral canal orientation relates to the spatial organization of the vestibulo-ocular reflex. The geometries of the semicircular canals and the extraocular muscles have been described as intrinsic coordinate systems, and, in order to maintain gaze during head motion, components of the head velocity vector are transformed into components of the angular eye velocity vector in the respective coordinate systems (Graf, 1988; Reisine et al., 1988). Even dur-

ing major reorganizations of cranial architecture, the relationship between the two coordinate systems is conserved, as is attested by the fact that the spatial orientation of the semicircular canals and the extraocular muscles is similar in lateral-eyed and frontal-eyed animals despite the radically different orientation of the optic axes (Ezure and Graf, 1984). In view of these constraints, it can be expected that selective forces maintain the planar relationship between the lateral canals and the medial and lateral rectus muscles during evolutionary changes of cranial morphology. This hypothesis can be tested most directly by comparing the orientations of both the semicircular canals and the extraocular muscles in a wide range of species on the basis of serial sections or medical imaging techniques such as CT or magnetic resonance imaging (MRI). Some indirect support for a muscle-canal correlation is provided by the observation that the lateral canal is particularly inclined relative to the external basicranial orientation in *Alouatta*, with a typically dorsally deflected (airorhynch) face, whereas it is particularly declined in *Papio* and *Theropithecus*, with ventrally deflected (klinorhynch) faces and orbits (LSCm < ba-na, Table 6). Along similar lines, Matano et al (1985, 1986) found that in contrast to the human-like orientation of the lateral canals in *Tarsius*, those of *Nycticebus* are particularly inclined, in accordance with its more superiorly facing eyes and orbits.

Apart from the interaction with the extraocular muscle system, planar stability of the vertical canals is likely maintained for a second reason. Each anterior canal and the approximately coplanar contralateral posterior canal work as a functional neurophysiological unit in the form of a push-pull pair, with head rotation resulting in excitation of one canal and inhibition of the other. Thus, drastic changes of the canal planes—for example, following reorientation of the petrous pyramids—would disturb the interplay between the left and right vestibular organs, and selective pressures may therefore result in stability. Only one labyrinth of each specimen was investigated in the present study, and therefore coplanarity of the vertical push-pull pairs cannot be verified at

present. If bilateral symmetry is assumed, it is only the two ateline species that stand out by showing the largest deviations of 16 and 21° from coplanarity. It is intriguing that in these two species the angle between the ipsilateral anterior and posterior canal is nevertheless similar to that in other anthropoids. Thus, this could indicate that the hydrodynamical interaction between the two ipsilateral canals is at least as important as the neurophysiological one between the contralateral push-pull pairs.

Planar stability of the semicircular canals in the cranium is a biologically important phenomenon, but its functional significance should not be exaggerated, given that the relevant angles typically show ranges of variation of over 20° in the human sample. However, angles that are more closely related to function, such as those between contralateral canals and extraocular muscles, may prove to be more constrained. The similarity of canal orientations in humans and African apes can be used as a practical tool when reconstructing fragmentary fossil hominid crania to obtain or check estimates of the midsagittal plane and to assist in associating facial and basicranial parts. As such, the labyrinth has already been used in the CT-based three-dimensional reconstruction of the Devil's Tower Neanderthal child (Zollikofer et al., 1995).

LABYRINTHO-BASICRANIAL RELATIONSHIPS

Comparative studies have previously noticed the correspondence in humans between the rotated morphologies of the posterior cranial base and the bony labyrinth in the sagittal plane and have suggested that this reflects interspecific correlations common to mammals in general (Villemin and Beauvieux, 1934; Delattre, 1951; Delattre and Fenart, 1960, 1961, 1962; Fenart and Debblock, 1973). The analyses in the present study now provide quantitative evidence that, at least among primates, such labyrintho-basicranial relationships do indeed exist. That the rotated morphology of the human labyrinth is consistent with the interspecific correlations suggests that it follows from general mechanisms of primate cranial development. In contrast, the apparent cor-

respondence in humans between the coronal orientations of the lateral canal axis of symmetry and the posterior petrosal surface cannot be associated with any interspecific correlation, and this aspect of the human labyrinth thus appears to represent a unique, truly independent trait.

Brain growth and development have been described as the predominant influence on endocranial aspects of basicranial morphology such as midline flexion (Ross and Ravosa, 1993, and studies cited therein) and petrous pyramid orientation (Dean, 1988). In particular, Ross and Ravosa (1993) found that among extant primates the degree of flexion is positively correlated with brain size relative to basicranial length, and Spoor (1997) subsequently showed a similar relationship for the midsagittal orientation of the foramen magnum and the transverse orientation of the petrous pyramids. These observations appear to corroborate the hypothesis that the highly flexed human basicranium with an inferiorly facing foramen magnum and coronally oriented petrous pyramids represents a spatial solution to accommodating a large brain in combination with a relatively short cranial base.

Bearing in mind the position of the otic capsule in between the developing cerebrum and cerebellum, it is likely that brain growth influences the overall shape not only of the basicranium but also of the labyrinth. This could thus represent the developmental basis for the interspecific correlations between labyrinthine and basicranial shape identified in this study. However, the influence of brain development on the labyrinthine shape and, for example, the petrosal surface or the clivus should not be seen as a synchronous process. The human labyrinth has fully attained its adult morphology when the ossification of the otic capsule is completed between the twenty-third and twenty-sixth week of fetal development (Bast, 1930; Anson and Donaldson, 1981). The endocranial aspects of the cranial base, on the other hand, obtain their final shape only after birth, interacting therefore with much later periods of brain growth.

The hypothesis that phylogenetical changes in brain morphology result in the deformation of specific aspects of the laby-

rinth has been proposed by Werner (1933). Using the term "mechanische Dislokationstheorie," Werner described the tilted or rotated orientations of the common crus and the ampullar line relative to the plane of the lateral canal in fishes and birds and briefly referred to the influence of cerebral expansion on the primate labyrinth. Werner (1933) also drew attention to a crucial aspect of the phenomenon that the labyrinth seems to deform rather than simply move (e.g., rotate) under the influence of external forces: the contrast between parts that change in orientation or shape and others that remain unaffected, the planar orientations of the semicircular canals in particular. Thus, if the differences in labyrinthine shape between humans and the African apes are brought about by distinct patterns of brain development prior to ossification of the otic capsule, this effect is apparently compensated for with respect to the planar orientations of the canals. That such compensatory processes may indeed occur is suggested by the ontogenetic movements of the human otic capsule in the transverse plane whereby an overall rotation of the labyrinth is counteracted by a rotation of the anterior canal in opposite direction (Bossy and Gaillard de Collogny, 1965).

Identifying the actual mechanisms of interaction between the growing brain and both the basicranial shape and the labyrinth requires a thorough understanding of the pattern and timing of the ontogenetic changes of these structures. However, little evidence is available, because the few studies that have dealt with the prenatal period of primate basicranial development do not consider soft-tissue morphology (Starck, 1961; Hofer, 1963; Bossy and Gaillard de Collogny, 1965; Levihn, 1967; Cousin, 1969; Sirianni and Newell-Morris, 1980; Dimitriadis et al., 1995). Some insight into a possible mechanism linking brain development with the sagittally rotated morphology of the human labyrinth is given by prenatal changes of the tentorium cerebelli. In the period before the otic capsule is ossified, the tentorium rotates backward and downward over 90° due to the expansions of the cerebral hemispheres (Dabelow, 1931; Hochstetter, 1939; Moss et al., 1956). The tentorium

being attached to the superior petrosal margin, this may result in a rotatory, deforming force on the cartilaginous otic capsule.

If interspecific diversity in brain growth and the associated degree of fetal tentorial rotation is indeed reflected in the labyrinth, it could perhaps be expected that labyrinthine angles are correlated with relative brain size, just as midline basicranial flexion is. However, an initial analysis using relative brain size values listed in Spor (1997) suggests that this is not the case. For example, large cercopithecoids show a more human-like, sagittally rotated labyrinth than the great apes do (Tables 7, 11), whereas their relative brain size is smaller. In this context, the ontogenetic process of change may be more relevant than the final result of adult brain size.

A possible mechanism influencing the petrous pyramid orientation is formed by the developing cerebellum enclosed in the posterior cranial fossa under the tentorium. Dean (1988) proposed that the short posterior cranial base in humans forces the cerebellum to expand laterally, which results in coronal reorientation of the petrous pyramids. Such a reorientation would obviously affect the fetal otic capsule, and Bossy and Gaillard de Collogny (1965) indeed found a 15° rotation of the human otic capsule prior to its ossification, with a simultaneous rotation of the cochlea and the anterior canal in the opposite direction. It is feasible that as a net effect of this complicated process the human lateral canal axis of symmetry turns coronally with the surrounding petrous pyramid, whereas other parts of the labyrinth tend to keep a more stable orientation. The fact that this is a unique trait of humans could, for example, be the consequence of a specific timing of lateral cerebellar expansion. Perhaps the marked increase in the lateral growth rate of the human cerebellum at the end of the fourth month (Noback and Moss, 1956) is part of such a mechanism, but it remains to be seen whether this pattern is typical for human brain development only.

CONCLUSIONS AND PROSPECTS

This paper set out to provide a comprehensive comparative review of the human bony labyrinth and to explore morphological diver-

sity of this structure in extant primates, in particular in relation to basicranial architecture and semicircular canal function. The morphology of the human labyrinth is found to be unique among extant primates with respect to the size of its semicircular canals as well as to aspects of its shape.

From the available evidence, it seems probable that the arc sizes of the semicircular canals are functionally linked with the type of head movements characteristic for an animal's locomotor behavior. However, it is clear that the specifically human canal proportions do not simply reflect habitual bipedalism but that other factors influencing head motility are likely involved as well. The evidence on canal function from biophysical models and comparative studies appears contradictory. A key to resolving this situation is to analyze actual frequency spectra of head movements in nonhuman primates so that theory can be tested more directly with empirical data. Moreover, a systematic survey of vertebrate labyrinthine morphology would contribute to a more precise empirical description of the link between semicircular canal dimensions and categories of locomotor behavior.

The planar orientations of the semicircular canals in the cranium tend to be similar among most primate species. The hypothesis that this stability largely follows from a close functional relationship with the extraocular muscles warrants further investigation. Such a spatial link between basicranial and facial areas would constitute an interesting biological constraint on any phylogenetic change of cranial morphology.

An intriguing aspect of the labyrinth is that its morphology is open to external developmental influences only prior to ossification of the otic capsule, in humans at the end of the second trimester of gestation. If interspecific shape differences do indeed follow from the differential interaction between the growing brain and basicranium, as has been suggested here, adult labyrinthine shape forms a snapshot of a limited period of fetal development. This would thus give the opportunity to assess evolutionary changes of prenatal cranial ontogeny on the basis of the labyrinth in extant and fossil taxa. Hypotheses regarding the developmen-

tal origin of the human labyrinthine shape will have to be tested through detailed quantitative analysis of fetal development of the basicranium and brain in humans and, where feasible, nonhuman primates.

The bony labyrinth may show a species-specific morphology, most clearly demonstrated here by humans and *Pongo*, and thus it can potentially be used to assess the phylogenetic affinities of fossil specimens. However, labyrinthine traits should be used with care in phylogenetic analysis because of possible homoplasies following from the functional association with vestibular function. Moreover, the high degree of correlation between different aspects of the labyrinth should be taken into account.

ACKNOWLEDGMENTS

We thank L. Aiello, B. Baljet, B. Davis, P. Jenkins, H. Kemperman, W. Mulder, R. Perizonius, C. Smeenk, A. Timmerman, P.V. Tobias, W. Van Neer, and G.N. Van Vark for access to specimens analyzed in this study and P. Liepins, J. Lynch, and M. Tighe for providing CT facilities. We are grateful to C. Dean, J. Moore, C. Ross, C. Ruff, and P. van Waes for helpful comments on the manuscript and to N. Jeffery for general assistance. The support of Philips Medical Systems is acknowledged.

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